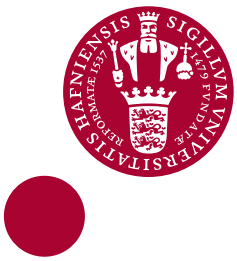

Before the flood

Miocene otoliths from eastern Amazon Pirabas Formation reveal a Caribbean-type fish fauna

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Before the flood: Miocene otoliths from eastern Amazon Pirabas Formation reveal a Caribbean-type fish fauna

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ABSTRACT

The Pirabas Formation of Early Miocene age represents the final stage of the central western Atlantic carbonate platform in northeastern South America, predating the emplacement of the Amazon delta system. The otolith-based fossil fish fauna is represented by 38 species typical of a shallow marine environment. A total of 18 species are described new to science from the families Congridae, Batrachoididae, Bythitidae, Sciaenidae and Paralichthyidae. The fish fauna was associated with high benthic and planktic primary productivity including seagrass meadows, calcareous algae and suspension-feeders. The break of todays shallow marine bioprovince at the Amazonas delta mouth is not evident from the fish fauna of the Pirabas Fm., which shows good correlation with the Gatunian/proto-Caribbean bioprovince known from an only slightly younger time window in Trinidad and Venezuela. Differences observed to those Early Miocene faunal associations are interpreted to be mainly due to stratigraphic and geographic and not environmental differences. We postulate that the emergence of the Amazonas river mouth close to its present day location has terminated the carbonate cycle of the Pirabas Fm. and pushed back northwards a certain proportion of the fish fauna here described.

1. Introduction

The knowledge of the seascape of Tropical America during the Neogene has increased significantly over the last two decades, particularly with respect to the ancient Western Amazonas hydrographic system (Hoorn et al., 2010), the large and biodiverse Proto Amazonian – Orinoquian fauna from the Urumaco trench of northwestern Venezuela (Sánchez-Villagra et al., 2010), the Huila Group in the upper Magdalena Valley of Colombia (Kay et al., 1997) and the Acre region in the western Amazon of Brazil (Hoorn et al., 2010). These studies and associated discussions have refined the understanding of the origin and nature of the fossil Amazonian fluvial – lacustrine fauna of northern South America. Amongst the aspects that have been discussed are the origin, direction and form of the western Amazon water flux into northern South America (e.g. Aguilera and Lundberg, 2010; Lundberg et al., 2010; Aguilera et al., 2013b, c), the existence and timing of marine incursions (e.g. Hoorn, 1993, 1994; Hoorn et al., 2010), the timing and rate of uplift of the Andes and its relation to the geographic, topographic and hydrographic changes in western South America (Rod, 1981; Díaz de Gamero, 1996; Hoorn et al., 2010; Figueiredo et al., 2009; Shephard et al., 2010), the oceanographic changes in relation to the closure of the Central American Seaway (Leigh et al., 2013; Jackson and O'Dea, 2013) and the origin of the modern-day Amazon River (Heinrich and Zonneveld, 2013).

We contribute to this discussion with a paleobiological analysis or the teleostean fish fauna reconstructed from otolith assemblages from the Pirabas Formation (Fm.) of eastern Amazon. In contrast to the terrestrial setting in the Western Amazon after the Middle Miocene, the lower Miocene Pirabas Fm., located at the present-day Amazon River delta mouth, was fully marine. The marine fish fauna presented here indicates strong affinities with the proto-Caribbean fish assemblages as described from Venezuela and Trinidad (Aguilera et al., 2011) and is interpreted as predating the emplacement of the Amazon delta system in this location.

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Miocene to Pleistocene fossil fish assemblages in the Tropical Western Atlantic (TWA) were largely controlled by oceanographic and geographic changes during the closure of the Isthmus of Panama and the geographic establishment of the lesser and greater Antilleans in the Caribbean Sea (Bachmann, 2001; Coates et al., 2005; Pindell et al., 2005; O'Dea et al., 2007; Schwarzhans and Aguilera, 2013), and the reconfiguration of the South American continental hydrographic drainage and the establishment of the large transcontinental western Amazon River flux to the Atlantic Ocean during Middle to Late Miocene (Silva et al., 1999; Figueiredo et al., 2009). Further factors having affected the composition of the fish fauna of the Pirabas Fm. in particular are related to the biogenic carbonate deposition during Early Miocene (Johnson et al., 2009; O'Dea et al., 2007) and the subsequent shift to deltaic siliciclastic sedimentation in the Amazon delta (Damuth and Kumar, 1975; Silva et al., 1999; Figueiredo et al., 2009; Watts et al., 2009).

Leigh et al. (2013) concluded in a review that the Caribbean paleobiogeographic history is a reflection of the faunal interactions, preferences of habitat and oceanographic variations between the Tropical Eastern Pacific (TEP) and the Tropical Western Atlantic along the marine Panamanian corridor from the latest Oligocene until the seaway closed about 3 Mya (Coates and Stallard, 2013; Jackson and O'Dea, 2013). At that time, Caribbean primary productivity declined dramatically as nutrient levels fell, while benthic productivity from expanding coral reefs, seagrass beds and bottom-dwelling calcareous algae became to dominate Caribbean coastal ecosystems we know today. The purpose of this study further is a detailed taxonomic description of Teleostean fish otoliths from the Pirabas Fm. of the pre-Amazon Delta, and an evaluation of their paleoenvironment and the paleogeographic implications.

2. Material and methods

The studied material was collected from outcrops located on the Atalaia beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 047° 18′ 55.6″ W) during minimal low tides (Fig. 1). The section was measured and the specimens were collected from an exposed section by picking from the surface along the stratigraphic sequence (Fig. 2). In addition, 30 kg of bulk samples were processed and sieved at the laboratory employing 2 mm, 1 mm and, for a smaller proportion, 0.5 mm mesh sizes.

The otoliths obtained commonly show effects of leaching on the surface and sometimes also some dark speckled pigmentation or mineralization, both probably due to the exposure of the rocks and the contained fossils to seawater at the sampling locality. This results in many specimens being rather poorly preserved and only about 50% of them being identifiable to species level. In consequence, rare species are mostly not well represented.

All specimens are deposited in the paleontological collection of the Museu Paraense Emilio Goeldi (MPEG-V), Brazil. The systematic classification and descriptive terminology has been adopted from Aguilera (2010). The specific identifications are based on comparative analyses with Recent and fossil collections housed at the Universidad Francisco de Miranda (UNEFM-PF) in Venezuela, the Smithsonian Tropical Research Institute in Panama (STRI-PPP-T), the collection of W. Schwarzhans in Hamburg, Germany and literature.

3. Geological setting

The Pirabas Formation (Maury, 1925) of Early Miocene, Aquitanian to Early Burdigalian age, represents the final stage of the central western Atlantic carbonate platform in northeastern

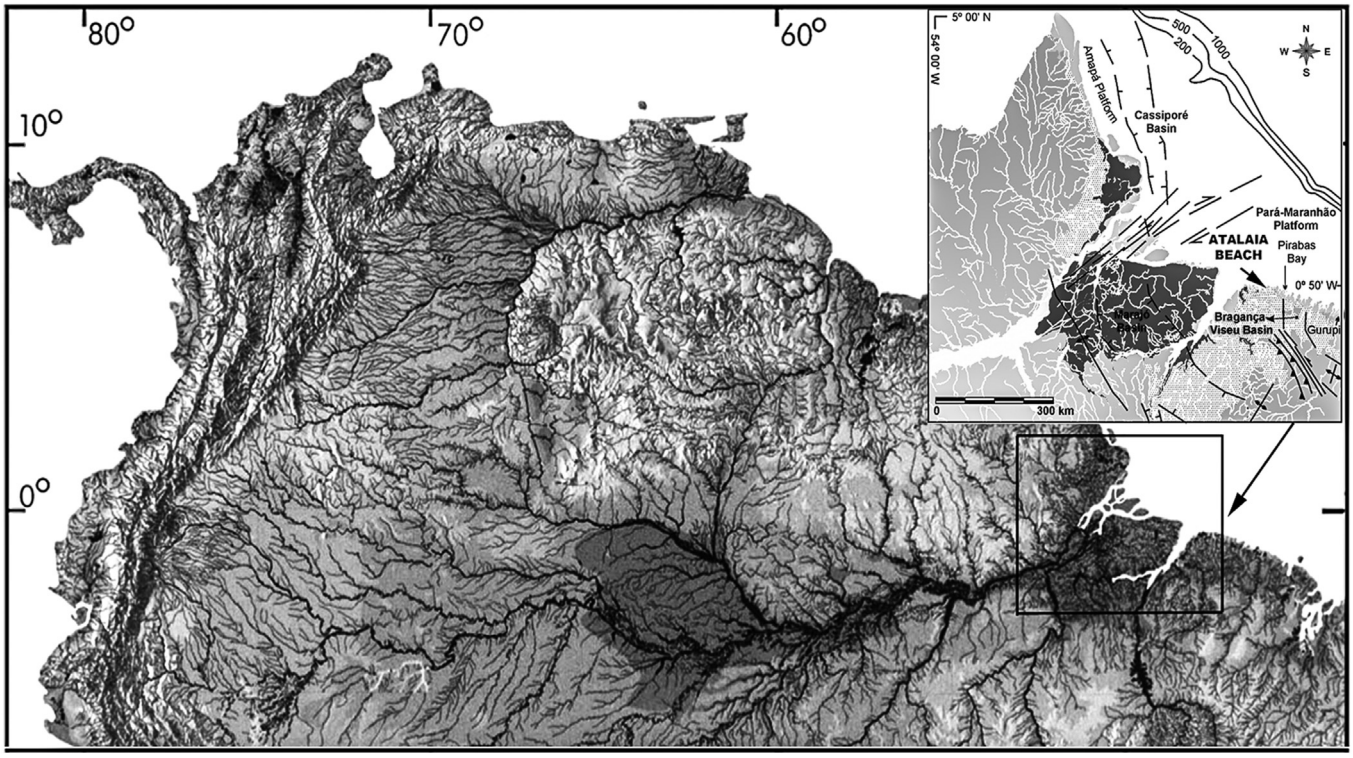

Fig. 1. Map of northern South America showing the location of the Atalaia Beach in the Amazon Delta and a regional geology map relevant for the fossils studied (base map modified from the U. S. Geological Survey and geology map modified from Aguilera et al., 2013a,b,c).

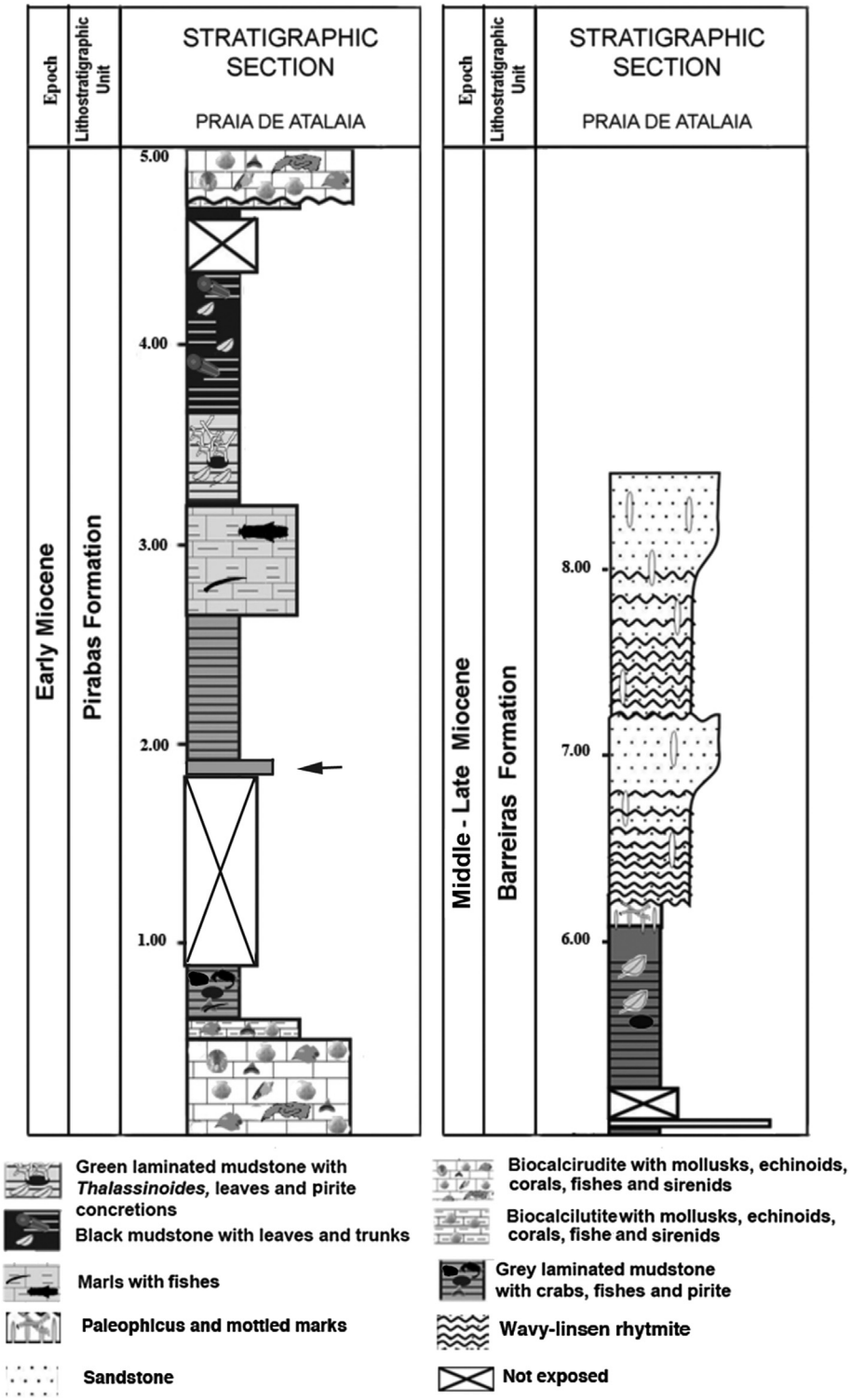

Fig. 2. Stratigraphic section of the Atalaia Beach outcrop. The arrow indicates the level with high otolith concentration. (base section modified from Aguilera et al., 2013a).

South America, directly overlain by deltaic siliciclastic sediments of the Amazon, Esequivo and Orinoco deltas following a drastic change of the hydrogeographic configuration that began in the Middle Miocene. It extends along the Pará, Maranhão and Piauí states of northern Brazil, and consists of carbonate coquina rocks of an offshore platform environment (grainstone and consolidated packstone, stratified wackestone to packstone and laminated mudstone). In addition, littoral facies (shoreface/foreshore), marginal lagoons, restricted platform environments (gray to olive mudstone and conglomeratic sandstone) and mangrove estuarine lagoons (dark mudstone, massif or laminated) have been recorded (Góes et al., 1990; Rossetti, 2001; Rossetti and Góes, 2004; Rossetti et al., 2013; Aguilera et al., 2013a, b).

The name Pirabas Formation was accepted as valid since 1925 (Léxico Estratigrafico do Brasil 1984). However, no stratotype section was selected by Maury (1925) from the type locality and until today no type section has been defined. Therefore, Góes et al. (1990), Rossetti and Góes (2004), Aguilera et al. (2013a, b) and Rossetti et al. (2013) summarized the geological descriptions and erected ten individual "non-type" sections from the Pirabas Fm. in the Pará state based on eight outcrops and two level mine excavations.

The formation is rich in fossils and was studied for the first time by Ferreira-Penna (1876). Paleontological work of White (1887) and Maury (1925) are the prime references for mollusk, bryozoan and coral faunas, and contributions by Petri (1954, 1957) for foraminifera, by Beurlen (1958a, 1958b) for crustaceans, by Santos (1958, 1967) for echinoids, Santos and Travassos (1960) for fishes and Paula-Couto (1967) for sirenians. Many further references for additional descriptions, records and/or reviews of different fossil taxa are summarized in Távora et al. (2010), Aguilera and Paes (2012) and Aguilera et al. (2013a, b). The planktonic foraminifera association from the Pirabas Fm. (Petri, 1957; Fernandes, 1984, 1988; Fernandes and Távora, 1990; Távora and Fernandes, 1999) correlates with the Early Miocene, Aquitanian to Early Burdigalian, N4–N5 global biozones (Blow, 1969). A palynological investigation of a sample from the Pirabas Fm. has revealed an age not younger than Early Miocene (C. Jaramillo). Fig. 3 shows a stratigraphic correlation chart of Pirabas Fm. with other formations of the Tropical American Neogene with otoliths records. The Atalaia shale and mudstone section, from which the fossils were mainly obtained, represents the uppermost level of the Pirabas Fm. just below the middle Miocene Barreira Fm. (Góes et al., 1990).

The paleoenvironment along the Atalaia section is interpreted as a transitional tidal platform, and begins with a rich infaunal and epifaunal invertebrate component associated with high algal and sea grass productivity (photic zone) within a sediment composed mainly of biocalcirudite with mollusks fossilized in "life" position. A biocalcilutite, rich in fossils, overlay the biocalcirudite and

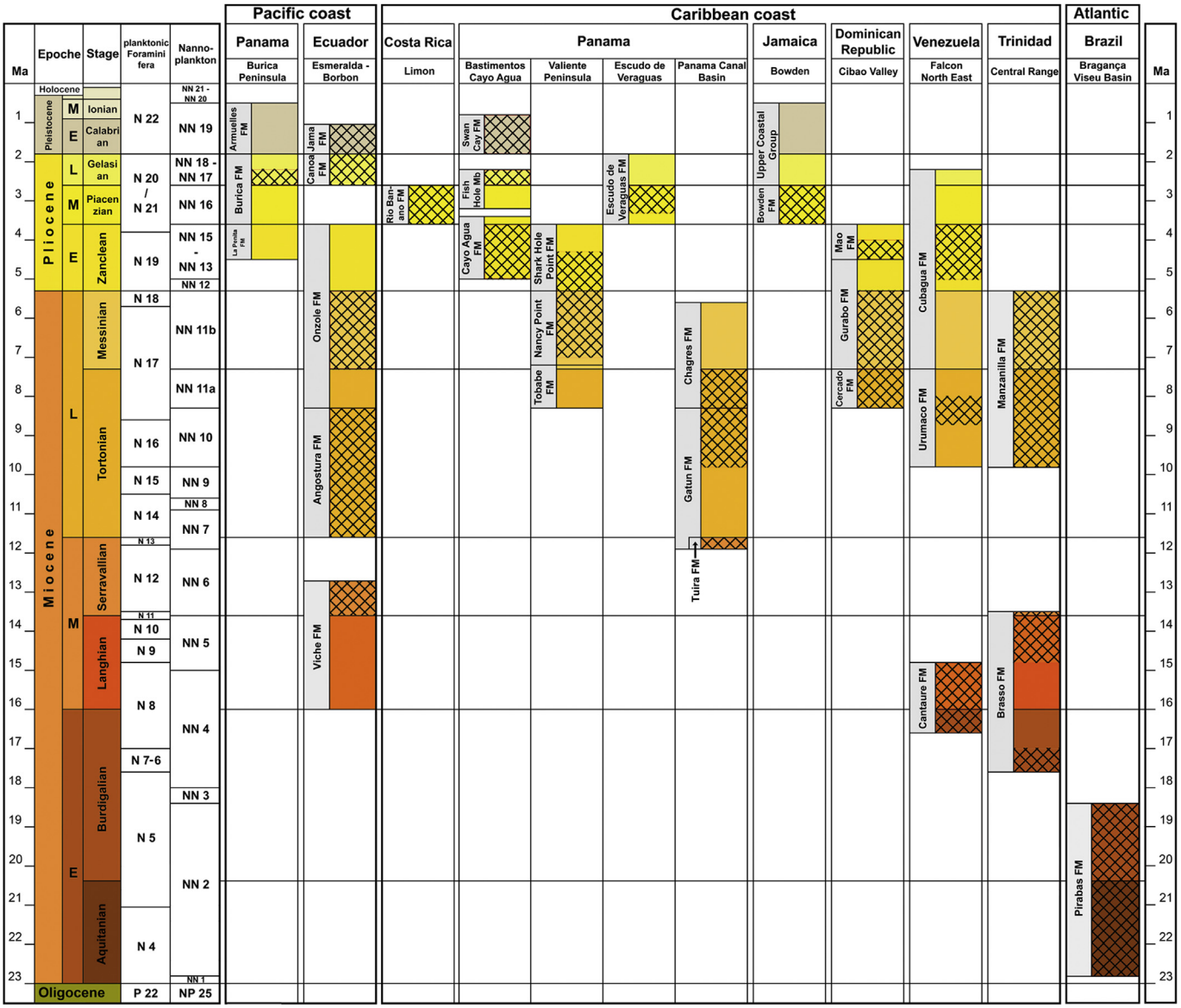

Fig. 3. Stratigraphic correlation chart depicting stratigraphic positions of otoliths studied (hatched) from Tropical America Neogene rocks (modified from Schwarzhans and Aguilera, 2013 with additional stratigraphy data from Brazil after Rossetti et al., 2013).

represents a sublittoral paleoenvironment that was exposed to waves and tidal influence. Gray laminated mudstones occurring abruptly over the biocalcilutite, when the tidal platform was replaced by very shallow coastal lagoon environment associated with a rapid burial subsidence and the deposition of siliciclastic sediments from the established early continental drainage. The paleoenvironment of the entire sequence is interpreted as transitional brackish/marine. The higher overlying green laminated mudstone indicate an inter-tidal paleoenvironment as evidenced by thalassinoid bioturbation and leaf imprints and a black mudstone further up section may represent a marginal lagoon with mangrove vegetation with leaf and wood remains. The top of the section consists of biocalcirudite coquina rocks deposited in tidal platform (photic zone), with abundant broken shells and echinoids fragments interpreted to be a result of tropical storms in the shallow sublittoral. Finally, the Atalaia sequence of the Pirabas Fm. is capped by the siliciclastic Barreira Fm. (Góes et al., 1990; Rossetti, 2001; Rossetti and Góes, 2004; Aguilera et al., 2013a).

4. Systematic paleontology

TELEOSTEI
Albulidae
Albula Scopoli, 1777

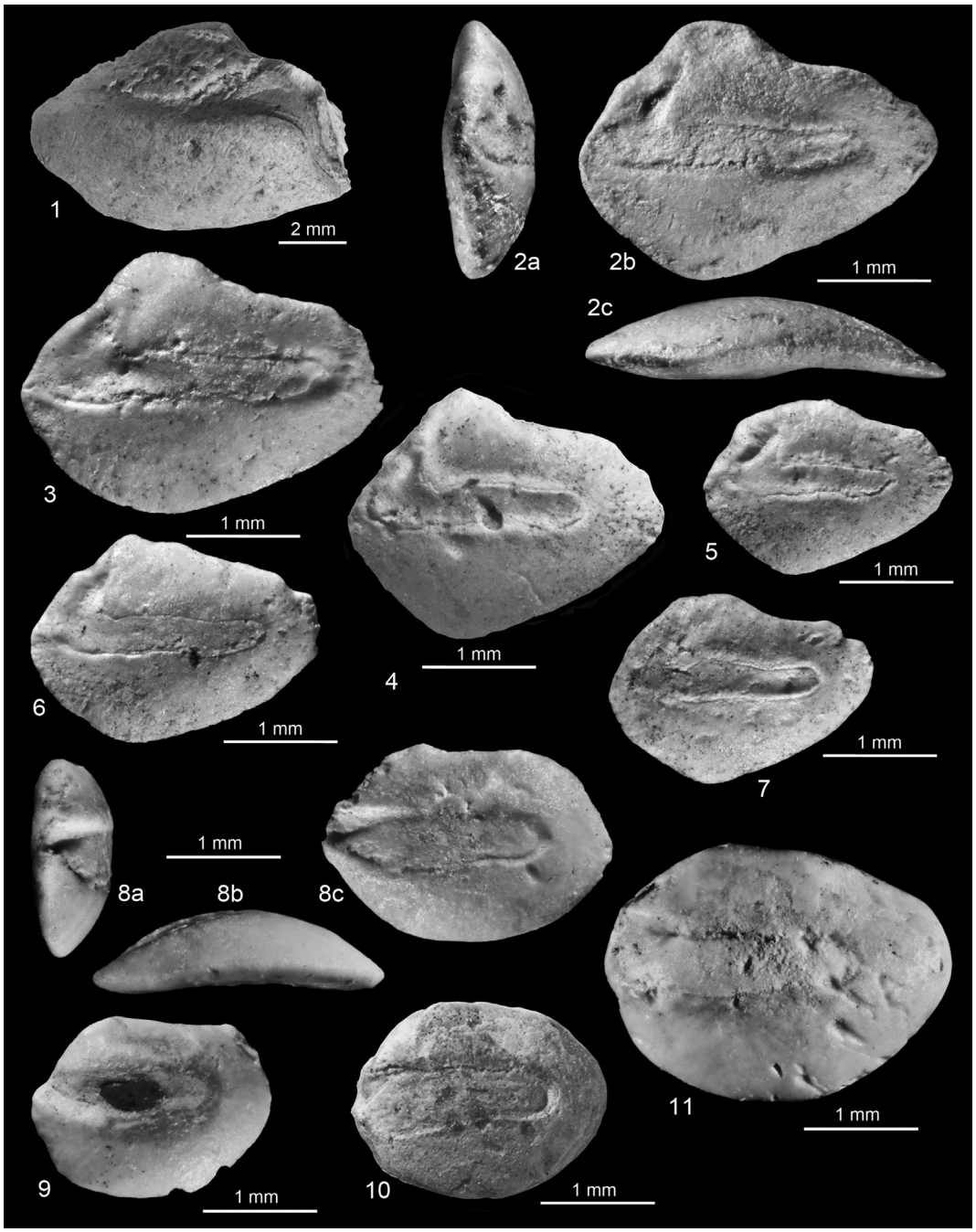

Fig. 4. 1 *Albula* sp. MPEG-1830-V; 2 †*Paraconger paraensis* n. sp., Holotype, MPEG-1829-V; 3–7 †*Paraconger paraensis* n. sp., Paratypes, MPEG-1931-V; 8 †*Pythonichthys pirabasensis* n. sp., Holotype, MPEG-1933-V; 9–11 †*Pythonichthys pirabasensis* n. sp., Paratypes, MPEG-1934-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

Albula sp.
Fig. 4.1
Material – MPEG-1830-V, two otoliths, from Atalaia Beach.
Discussion – Poorly preserved and eroded otoliths that cannot be identified to species level.

Congridae
Paraconger Kanazawa, 1961
Paraconger paraensis n. sp. Aguilera and Schwarzhans
Fig. 4.2–4.7
Type material – Holotype, MPEG-1829-V (Fig. 4.2), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1931-V, eight specimens, same data as holotype.
Further material – MPEG-1932-V, 60 specimens, same data as holotype.
Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).
Etymology – Named after the Pará State, Brazil.
Diagnosis – OL: OH = 1.25–1.35. Sulcus narrow, its length more than 5 times sulcus height at center of sulcus. Predorsal projection sharp, anterior of middle of otolith; symmetrical to angular preventral angle; posterior tip rounded, moderately projecting.
Description – Otoliths rhomboidal in outline, with pronounced and sharp predorsal projection and preventral angle, moderately thick and slightly more than 3 mm long. Dorsal rim slightly depressed behind predorsal projection, otherwise gently curved. Ventral rim smooth, gently curved, except for rather sharp preventral angle. Anterior tip angular, but blunt and high; posterior tip narrower, regularly rounded, moderately projecting. Inner face convex, ventrally smooth, without distinct ventral furrow, dorsally with indistinct depression above middle part of sulcus. Sulcus long, narrow, positioned slightly supramedian, reaching close to anterior tip of otolith and terminating at moderate distance from posterior tip of otolith. Ostium and cauda not differentiated. Short dorsally directed, often somewhat depressed ostial channel present. Cauda slightly swinging with a ventrally somewhat widened tip, typical for otoliths of the *Ariosoma* genus group. Outer face flat to slightly concave, smooth.
Discussion – The otoliths of *P. paraensis* are readily distinguished from the three Recent species occurring in the tropical Atlantic – *P. caudilimbatus* (Poey, 1867) and *P. guianensis* Kanazawa, 1961 (figures in Nolf and Aguilera, 1998) both from the western Atlantic and *P. notialis* Kanazawa, 1961 (figure in Veen and Hoedemakers, 2005) from the eastern Atlantic – through the more compressed shape of the otolith and the much more slender sulcus. In this respect the Middle Eocene *P. sauvagei* (Priem, 1906) is more similar, differing mainly in a more regularly rounded preventral angle and a longer cauda reaching closer to the posterior tip of the otolith. Nolf and Aguilera (1998) figured a more slender otolith (OL: OH = 1.5) with a moderately narrow sulcus and a rounded preventral rim from the Early Miocene of Venezuela as representing the Recent *P. guianensis*.

Heterenchelyidae
Pythonichthys Poey, 1868
Pythonichthys pirabasensis n. sp. Aguilera and Schwarzhans
Fig. 4.8–4.11
Type material – Holotype, MPEG-1933-V (Fig. 4.8), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1934-V, five specimens, same data as holotype.
Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).
Etymology – Named after the location Pirabas, Pará State, Brazil.
Diagnosis – OL: OH = 1.3–1.5. Sulcus wide, with regular outline, its length about 3 times sulcus height at anterior third of sulcus. Undivided colliculum level with convex and smooth inner face, anteriorly reduced and pointed within much wider sulcus. All rims regularly curved, dorsal rim slightly shallower than ventral rim.
Description – Otoliths elongate, oval in outline, without pronounced angles, moderately thick and up to 3 mm long. Dorsal rim shallower than ventral rim, sometimes slightly depressed at middle. Ventral rim smooth, gently and regularly curved. Anterior and posterior rims regularly rounded. Inner face strongly convex, smooth, without ventral furrow and with very indistinct dorsal depression. Sulcus long, rather wide, slightly wider anteriorly than posteriorly, positioned slightly supramedian, almost open to anterior tip of otolith and terminating at moderate distance from posterior tip of otolith. Ostium and cauda not differentiated, uniform in outline. Undivided colliculum well expressed, level with inner face, anteriorly narrowed with a pointed tip, leaving dorsal and/or ventral space inside anterior part of sulcus without collicular filling. Outer face flat to slightly concave, smooth.
Discussion – Heterenchelyid otoliths exhibit only few characters useful for specific identification. In the case of *P. pirabasensis* it is primarily the anteriorly reduced and pointed colliculum within the much wider anterior part of the sulcus that faultlessly distinguishes this species from other known Recent or fossil heterenchelyids.

Ariidae
Aspistor Jordan and Evermann, 1898
Aspistor sp.
Fig. 5.1 and 5.3
Material –MPEG-1832-V, one lapillus otolith and MPEG-1913-V five lapilli otoliths, Atalaia Beach.
Diagnosis – These otoliths of *Aspistor* are distinguished from extant *Aspistor* species by a well-developed mesial inward curvature forming a wedge oriented posteriorly (vs. poorly developed or absent in Recent species), oval otolith contour and a not expanded anterior distal ditch.
Description – Oval shaped otolith. Anterior margin of otolith slightly concave. Anterior distal ditch not expanded and slightly rounded. Antero-mesial projection short and acute. Slight angular central mesial margin. Umbo located on anterior part of dorsal surface. Dorsal surface irregular and convex. Ventral surface smooth and convex. Pseudocauda of mesial shallow depression slightly curved posteriorly. Mesial inward curvature forming a well-developed wedge oriented posteriorly. Ratio lapillus length to width = 1.2–1.3. Ratio lapillus length to thickness = 2.3–2.7.
Discussion – A single skull-based species (†*A. verumquadriscutis* Aguilera and Marceniuk 2012) is known from the Late Miocene of the Caribbean, as well as two Recent species, *A. quadriscutis* (Valenciennes, 1840) and *A. luniscutis* (Valenciennes, 1840), both inhabiting estuarine and brackish waters of the eastern South American coast. The fossil specimens from the Pirabas Fm. can be distinguished from extant *Aspistor* species by a well-developed mesial inward curvature forming a wedge oriented posteriorly, oval otolith contour and a not expanded anterior distal ditch. Due to the lack of well preserved fossil specimens and ongoing research work of extant species (A. Marceniuk pers. com.) they are left in open nomenclature for the time being.

Bagre Cloquet, 1816
†*Bagre protocaribbeanus* Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira, 2013
Fig. 5.7–5.10
1998 *Arius* sp. – Nolf and Aguilera: pl. 3, figs. 1–5
2013 *Bagre protocaribbeanus* – Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira: figs. 11–12

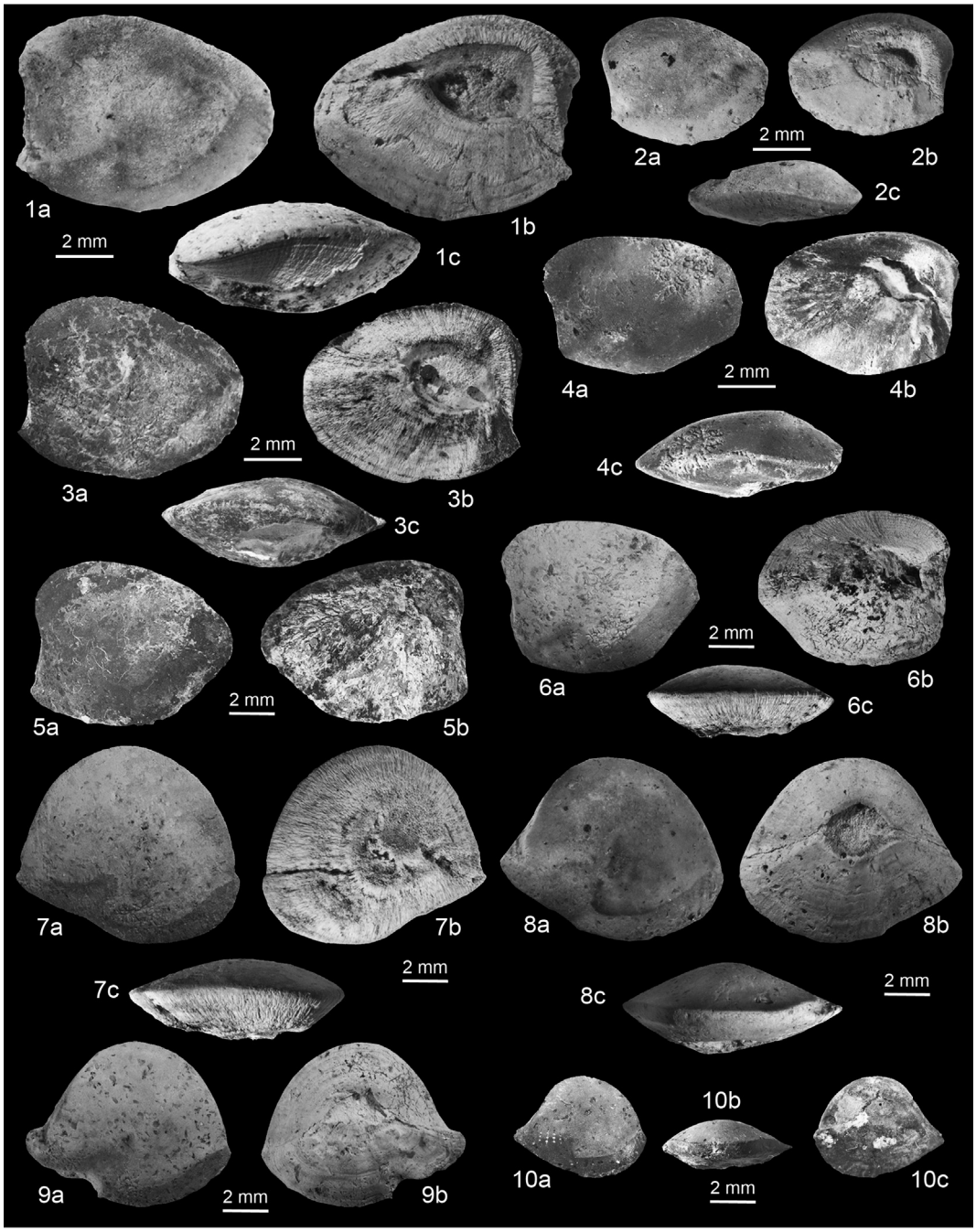

Fig. 5. 1, *Aspistor* sp., MPEG-1832-V; 3 *Aspistor* sp., MPEG-1913-V; 2,4 †*Cantarius nolfi,* MPEG-1783-V; 5 *Notarius* sp., MPEG-1784-V; 6 *Notarius* sp. MPEG-1912-V 7–10 †*Bagre protocaribbeanus,* MPEG-V-1781-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

Material – MPEG-V-1781-V, five lapilli otoliths; MPEG-V-1782-V, eight lapilli otoliths, Atalaia Beach.

Description – Otoliths broad and clam-shaped with circular outline, and sharp antero-mesial projection. Umbo located on anterior part of irregular and strongly convex dorsal surface. Ventral surface slightly convex. Pseudocauda of mesial shallow depression forming an arch. Mesial inward curvature forming a long, narrow expansion, which is oriented posteriorly. Mesial notch deep and wide. Ratio lapillus length to width = 1.1–1.3. Ratio lapillus length to thickness = 1.3–2.9.

Discussion – †*Bagre protocaribbeanus* is known from the lower Miocene Cantaure and Castillo formations in Venezuela, and lower Miocene Castilletes Formation in Colombia (Aguilera et al., 2013a).

†*Cantarius*, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira, 2013

†*Cantarius nolfi* Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira, 2013

Fig. 5.2 and 5.4

1998 *Genidens* sp. – Nolf and Aguilera: pl. 4, figs. 1–4

1998 *Arius* sp. – Monsch: pl. 4, figs. 19–20

2013 *Cantarius nolfi* – Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira: figs. 8 and 10

Material – MPEG-1783-V, five lapilli otoliths, Atalaia Beach.

Description – Regularly oval and extremely thick otoliths. Anterior margin slightly concave. Caudal margin rounded. Antero-mesial projection small and rounded. Umbo located on anterior part of dorsal surface. Dorsal surface irregular and very convex. Ventral surface convex. Pseudocauda of mesial shallow depression forming an arch and expanded posteriorly. Mesial inward curvature forming a well-developed wedge oriented posteriorly. Ratio lapillus length to width = 1.1–1.5. Ratio lapillus length to thickness = 1.8–2.6.

Discussion – †*Cantarius nolfi* is known from the lower Miocene Cantaure and Castillo formations in Venezuela, lower Miocene Castilletes Formation in Colombia and middle Miocene Pebas Formation in Colombia and Peru (Aguilera et al., 2013a).

Cathorops Jordan and Gilbert, 1882

†*Cathorops goeldii* Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira, 2013

No figure (see Aguilera et al., 2013, fig. 4)

2013 *Cathorops goeldii* – Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira: fig. 4a–e

Material – MPEG-1526-V, skull and associated pectoral girdle, Atalaia Beach.

Description – See Aguilera et al. (2013) for detailed description of skull and associated pectoral girdle.

Discussion – †*Cathorops goeldii* represent the earliest *Cathorops* fossil record and possibly predates the New World *Cathorops* diversification observed today, which is thought to have originated during the Early Pliocene (Betancur-R. et al., 2012). Therefore, it is argued that †*C. goeldii* may be regarded as an offshoot from the main *Cathorops* stem lineage (Aguilera et al., 2013a).

Cathorops sp.

2013 *Cathorops* sp. – Aguilera, Moraes-Santos, Costa, Ohe, Jaramillo and Nogueira: fig. 7a–b

No figure (see Aguilera et al., 2013, fig. 4).

Material – MPEG-1523-V, one lapilli otolith, Atalaia Beach.

Description – Macula-shaped to almost rectangular otolith. Anterior margin incurved. Dorsal surface smooth and convex. Ventral surface concave. Antero-distal ditch deep, continuing to anterior margin. Pseudocauda of mesial shallow depression expanded posteriorly. No mesial inward curvature developed. Ratio lapillus length to width = 1.4. Ratio lapillus length to thickness = 2.8.

Notarius Gill, 1863

Notarius sp.

Fig. 5.5 and 5.6

Material – MPEG-1784-V, one lapillus otolith and MPEG-1912-V, two lapilli otoliths, Atalaia Beach.

Description – Trapezoid lapillus otolith shape. Anterior margin of otolith slightly concave. Anterior distal ditch rounded and anterior antero-mesial projection short. Postero-mesial margin with an obtuse angle. Umbo located on anterior part of dorsal surface. Dorsal surface irregular and convex. Ventral surface smooth and convex. Pseudocauda of mesial shallow depression forming a wide arch expanded posteriorly. Mesial inward curvature and mesial notch situated more anterior than the central position of mesial margin. Ratio lapillus length to width = 1.2–1.3. Ratio lapillus length to thickness = 2.7.

Discussion – Otoliths are known from the extant Western Central Atlantic *N. neogranatensis* (Acero and Betancur-R. 2002) from the Caribbean coast of Colombia and nearby river mouths and *N. grandicasis* (Valenciennes, 1840) from the Gulf of Venezuela to the mouth of the Amazon River. The specimens from the Pirabas Fm. are left in open nomenclature for the time being due to the lack of specimens preserved well enough to serve as type-specimens.

Carapidae

Carapus Rafinesque, 1810

Carapus sp.

Fig. 6.1–6.2

Material – MPEG-1788-V, six otoliths, Atalaia Beach.

Description – Massive otoliths, oval in shape, with short, but pointed posterior tip. Inner face completely flat and outer face strongly convex. Dorsal and ventral rims almost equally curved, but dorsal rim thick and ventral rim sharp. Sulcus long, narrow, ventrally flat, filled with undivided colliculum.

Discussion – Poorly preserved and eroded otoliths that cannot be identified to species level.

Ophidiidae

Otophidium Gill in Jordan, 1885

Otophidium sp.

Fig. 6.3

Material – MPEG-1786-V and MPEG-1819-V, two otoliths, Atalaia Beach.

Discussion – Two poorly preserved otoliths of compressed ovoid shape, deep ventral rim and narrow sulcus. These characteristics allow assignment to the genus *Otophidium* despite their strong erosion. Two fossil otolith-based species of the genus *Otophidium* have been described from the Late Miocene of the Dominican Republic by Nolf and Stringer (1992) – *O. robinsi* and *O. robustum* – both of which show a more regular outline with a less deeply curved ventral rim.

Bythitidae Gill, 1861

Ogilbia Jordan and Evermann, in Evermann and Kendell, 1898

Ogilbia brasiliensis n. sp. Aguilera and Schwarzhans

Fig. 6.4–6.5

Type material – Holotype, MPEG-1787-V (Fig. 6.4), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1935-V, three specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Referring to the country of Brazil.

Diagnosis – OL: OH = 1.25; OL: SuL = 1.85; OcL: CcL = 2.25; OcH: CcH = 1.85. Dorsal rim with broad, regularly curved postdorsal angle.

Description – Moderately elongate, oval otolith of about 3.5 mm length. Ventral rim smooth, regularly and gently curved, deepest at its middle; dorsal rim with rounded predorsal angle and broadly rounded postdorsal angle. Anterior tip slightly pointed, with moderate concavity dorsally; posterior tip broad, slightly pointed and somewhat undulating dorsally. Inner face slightly convex with short, slightly inclined sulcus terminating at some distance from anterior and posterior tips. Ostium and cauda well separated; ostium much wider than cauda; cauda relatively long and narrow. Dorsal depression narrow, indistinct; ventral furrow distinct, moderately close to ventral rim of otolith. Outer face slightly convex, smooth.

Discussion – Otoliths of Recent species of the genus *Ogilbia* are difficult to distinguish and it might very well be that not all species can be identified by means of otoliths (Møller et al., 2005). *Ogilbia brasiliensis*, however, is recognized by the combination of a short sulcus with a wide ostium and a relatively long cauda, a moderately compact outline and a broadly rounded postdorsal angle. Of the Recent species from the western Atlantic those of *O. cayorum* Evermann and Kendall, 1898 are probably the most similar, with

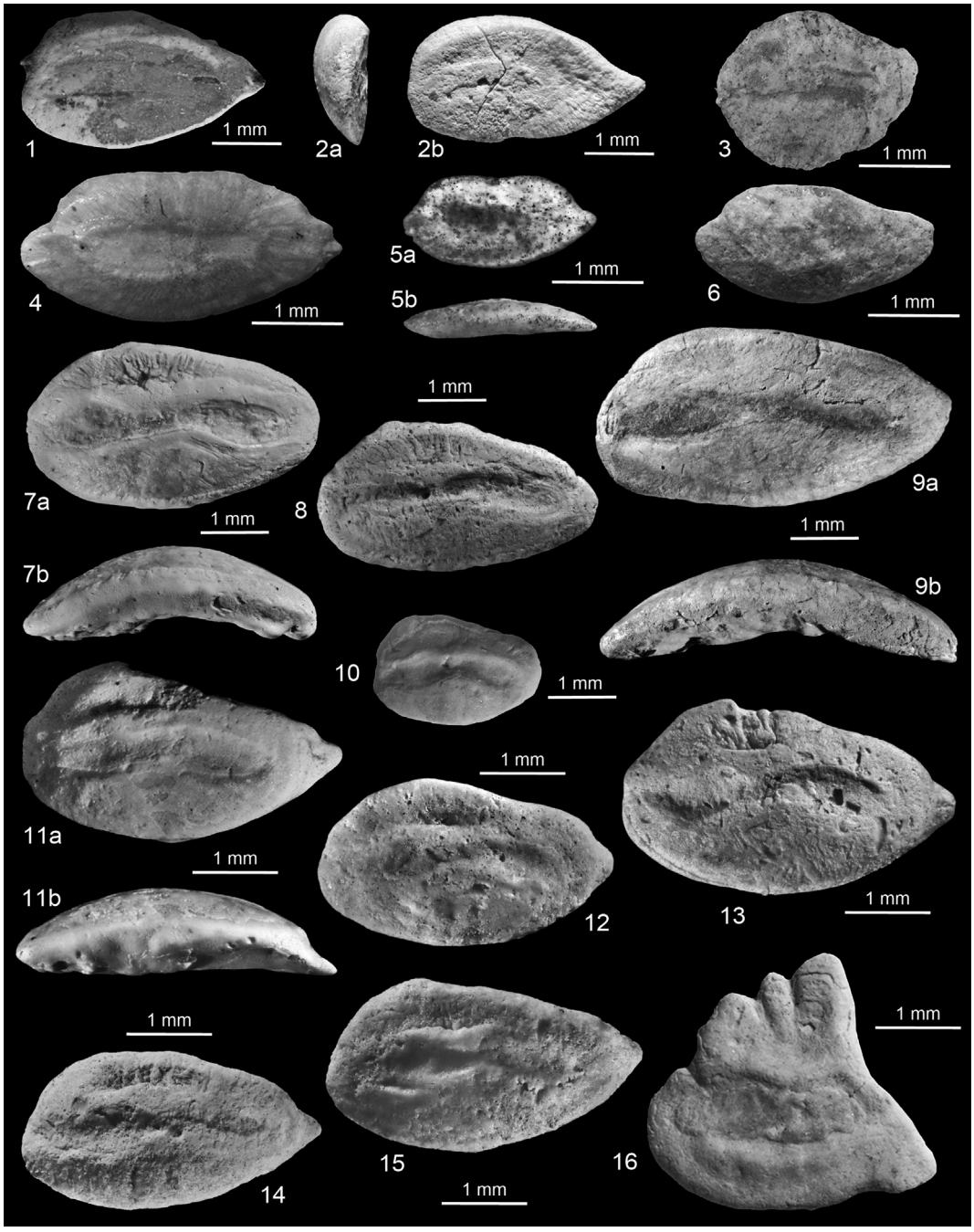

Fig. 6. 1–2 *Carapus* sp., MPEG-1788-V; 3 *Otophidium* sp., MPEG-1786-V; 4 †*Ogilbia brasiliensis* n. sp., Holotype, MPEG-1787-V; 5 †*Ogilbia brasiliensis* n. sp., Paratype, MPEG-1935-V; 6 *Ogilbichthys* sp., MPEG-1914-V; 7 †*Batrachoides confluentus* n. sp., Holotype, MPEG-1825-V; 8–10 †*Batrachoides confluentus* n. sp., Paratypes, MPEG-1916-V; 11 †*Batrachoides gracilentus* n. sp., Holotype, MPEG-1785-V; 12-15 †*Batrachoides gracilentus* n. sp., Paratypes, MPEG-1915-V; 16 †*Porichthys atalaianus* n. sp., Holotype, MPEG-1823-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

O. brasiliensis differing mainly in the longer and narrower cauda and the more rounded postdorsal angle. *Ogilbia brasiliensis* and *Ogilbichthys* sp. described in the following extend the areal distribution of the Dinematichthyini westwards and southwards of Trinidad, the nearest record in the Recent. Dinematichthyins are reef associated fishes not occurring along clastic shores or in the vicinity of major river discharge systems, thereby supporting the Pirabas Fm. to predate the establishment of the modern Amazonas river mouth.

Ogilbichthys Møller, Schwarzhans and Nielsen, 2004
Ogilbichthys sp.

Fig. 6.6

Material – MPEG-1914-V, one otolith, Atalaia Beach.

Discussion – A single, 2.6 mm long somewhat eroded otolith, which is characterized by an anteriorly expanded, rounded dorsal rim and a broad postdorsal depression as well as a short sulcus with its ostium and cauda barely separated. In fact it appears that the sulcus outline is continuous and the separation of the colliculi is the only effect showing a differentiation into ostium and cauda, similar to a few Recent species of the genus such as *O. kakuki* and *O. puertoricoensis* (Møller et al., 2004), while the majority of the extant species of the genus show fused colliculi.

Batrachoididae

Otoliths of the family Batrachoididae have been rare elements in all fossil otolith-based teleost faunas so far. At Atalaia Beach they represent the second largest group by number of species (seven) and specimens after the Sciaenidae.

Batrachoides Lacepède, 1800

Batrachoides confluentus n. sp. Aguilera and Schwarzhans

Fig. 6.7–6.10

Type material – Holotype, MPEG-1825-V (Fig. 6.7), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1916-V, nine specimens, same data as holotype.

Further material – MPEG-1936-V, five specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From confluentus (Latin) = confluence, meeting, referring to the intermediate position of the otolith morphology.

Diagnosis – OL: OH = 1.5–1.9, increasing with size; CcL: OcL = 1.15–1.3. Dorsal rim shallow, with broad, weakly developed predorsal lobe; ventral rim shallow; posterior tip rounded to slightly pointed, dorsally pronounced. Otolith distinctly curved in view from ventral. Sulcus with equally wide ostium and cauda, widely separated colliculi and cauda being slightly longer than ostium.

Description – Moderately thick, elongate otoliths with distinctly convex inner and concave outer faces up to 5.5 mm length. OL: OH increasing from 1.5 to 1.9 with size. Dorsal rim shallow, regularly curved with broad, weakly developed predorsal projection. Ventral rim smooth, shallow, gently curving, deepest at its middle. Anterior tip broadly rounded or blunt; posterior tip rounded or slightly pointed, then dorsally pronounced. Inner face strongly bent. Sulcus nearly median, moderately shallow, long, with convexly curved dorsal margin. Collum marked by broad, moderately strong incursion of ventral margin and equivalent, much less deep incursion of dorsal margin. Ostium and cauda well distinguished with rather widely separated colliculi. Cauda slightly longer than ostium, both widened at their terminal section. Ostium reaching close to anterior tip of otolith and cauda also reaching fairly close to posterior rim. Dorsal depression narrow, short, moderately distinct, separated from sulcus by rather narrow crista superior. Ventral furrow variable, feeble to distinct, close to ventral rim of otolith. Outer face rather smooth with few broad transversal ridges, distinctly concave in large specimens, almost flat in small specimens.

Discussion – The feeble predorsal projection, strong curvature of inner and outer faces, the nearly symmetrical sulcus with the ostium being slightly shorter than the cauda and the clearly separated colliculi all characterize these otoliths as representatives of the genus *Batrachoides*. Of the Recent species available for comparison in the collection of the senior author – *B. goldmani* Evermann and Goldsborough, 1902, *B. liberiensis* (Steindachner, 1867), *B. pacifici* (Günther, 1861), *B. surinamensis* (Bloch and Schneider, 1801) and *B. waltersi* Collette and Russo, 1981 – *B. waltersi* resembles *B. confluentus*, but *B. confluentus* differs in the more gently curving rims, the cauda being less than 1.3 times the length of the ostium (vs 1.5) and in being more thickset.

Batrachoides gracilentus n. sp. Aguilera and Schwarzhans

Fig. 6.11–6.15

Type material – Holotype, MPEG-1785-V (Fig. 6.11), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1915-V, 11 specimens, same data as holotype.

Further material – MPEG-1937-V, five specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From gracilentus (Latin) = slender, referring to the slender shape of the otolith.

Diagnosis – OL: OH = 1.8–1.9. Sulcus with narrow ostium, with curved dorsal rim; CcL: OcL = 1.2–1.5. Dorsal rim shallow, with broad, moderately developed predorsal lobe; ventral rim shallow; posterior tip pointed. Otolith moderately curved in view from ventral, with flat outer face.

Description – Robust, elongate otoliths with markedly convex inner face and flat to slightly concave outer face up to 4 mm length. Dorsal rim shallow with broad, moderately developed, anteriorly positioned predorsal projection. Rear part of predorsal projection sometimes coarsely ornamented. Ventral rim smooth, shallow, gently curving, deepest at its middle. Anterior tip broadly rounded, bent outwards; posterior tip pointed. Inner face markedly bent, but not nearly as much as Recent species of the genus or the co-occurring *B. confluentus*. Sulcus slightly supramedian, moderately deep, long, with curved, convex dorsal margin and broad incursion at ventral margin. Ostium and cauda poorly distinguished with its colliculi positioned relatively close at collum, sometimes appearing as almost fused. Sulcus widened at its middle at highest position of sulcus margin, terminating at moderate distance from posterior tip of otolith. Cauda about 1.2–1.5 times as long as ostium; ostium narrower, tapering anteriorly without clear opening. Dorsal depression above ostium and anterior half of cauda, distinct and deep ventrally, separated from sulcus by broad crista superior. Ventral furrow feeble, close to ventral rim of otolith. Outer face flat to very slightly concave and smooth.

Discussion – These otoliths are placed into the genus *Batrachoides* based on the slender outline with the low predorsal projection and the pointed tip and the long sulcus with its ostium being clearly shorter than the cauda. Most Recent species from tropical America are characterized by a very strongly bent inner face and a strongly concave outer face and also usually show a rather wide ostium. It differs from all known Recent otoliths of the genus in the pointed posterior tip, the more pronounced predorsal lobe and the nearly flat outer face. The one coming closest in otolith morphology is *B. surinamensis* (Bloch and Schneider, 1801), Recent in the Caribbean from Honduras to Brazil. Its otoliths share with those of *B. gracilentus* the nearly fused colliculi, the slender shape and the moderate curvature of inner and outer faces. *Batrachoides gracilentus* differs from the parallel occurring *B. confluentus* in the pointed posterior tip, the more pronounced predorsal projection and the lesser curvature of inner and outer faces.

Porichthys Girard, 1855

Porichthys atalaianus n. sp. Aguilera and Schwarzhans

Fig. 6.16

1976 *Porichthys* sp. – Nolf: pl.4, figs. 2–4

Type material – Holotype, MPEG-1823-V (Fig. 6.16), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratype, MPEG-1917-V, one specimen, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Named after the type locality Atalaia Beach.

Diagnosis – OL: OH = 1.1. Dorsal rim very high with highest point posteriorly, anteriorly coarse crenulated; ventral rim shallow; posterior tip distinctly inferior, very pointed and projecting. Sulcus large, with nearly fused colliculi and broad caudal pseudocolliculum.

Description – Moderately thick, very compressed high bodied otoliths up to 3.5 mm length. Dorsal rim very high, with highest point posteriorly above tip of cauda and anteriorly inclined and coarsely crenulated. Ventral rim smooth, shallow, anteriorly gently curving, posteriorly straight to slightly concave. Anterior tip inferior, broadly and regularly rounded; posterior tip shifted ventrally to joint with ventral rim and developed as pointed, massive projection. Inner face nearly flat. Sulcus slightly inframedian, shallow, wide, long, reaching close to anterior and posterior tips of otolith. Ostium and cauda poorly distinguished, ostium about as wide as cauda inclusive caudal pseudocolliculum. Colliculi poorly differentiated, almost fused; caudal pseudocolliculum broad. Dorsal depression wide, with rather indistinct margins; few radial furrows reaching onto dorsal field from deep, coarse crenulation of anterior part of dorsal rim. Ventral furrow a broad, blurred depression. Outer face slightly convex with few radial furrows on dorsal field.

Discussion – The genus *Porichthys* and the related monospecific genus *Aphos* contain highly characteristic otoliths in outline and sulcus organization. They are the only ones known outside Myctophidae with a caudal pseudocolliculum, albeit wide and flat in this case and not ridge like with sharp ventral rim as in myctophids. Recent *Porichthys* otoliths show two related patterns, one more elongated with an OL: OH ratio of about 1.3–1.6 often with development of a deep mediodorsal incision of the dorsal rim, the other more compressed with an OL: OH ratio between 0.9 and 1.2 and usually not exhibiting a depression of the dorsal rim. *Porichthys atalaianus* belongs to the second group, which in the Recent is mostly known from the Pacific shores of tropical America for instance *P. greenei* Gilbert and Starks, 1905, *P. margaritatus* (Richardson, 1844), *P. mimeticus* Walter and Rosenblatt, 1988 and *P. plectrodon* Jordan and Gilbert, 1882. The proportions of the otolith and the outline of *P. atalaianus* resemble most the Pacific *P. margaritatus*, while *P. greenei* have the most compressed, high bodied otoliths (OL: OH = 0.9–0.95) and *P. mimeticus* and *P. plectrodon* are both slightly more elongate (OL: OH about 1.2). The very pronounced postventral projection distinguishes *P. atalaianus* from the mentioned species, while the posteriorly pronounced dorsal rim resembles that of *P. greenei*. Specimens recorded from Nolf (1976) as *Porichthys* sp. from slightly younger, Late Burdigalian to Middle Langhian strata of Trinidad represent the same species. Another undescribed and rather different species with a more stretched, nearly triangular outline has been figured as *Porichthys* sp. from the Early Langhian Cantaure Fm. of Venezuela by Nolf and Aguilera (1998).

Sanopus Smith, 1952

Sanopus mendax n. sp. Aguilera and Schwarzhans

Fig. 7.1–7.3

Type material – Holotype, MPEG-1938-V (Fig. 7.1), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1939-V, six specimens, same data as holotype.

Further material – MPEG-1940-V, nine specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From mendax (Latin) = mendacious, deceptive, referring to the smooth, level inner face which is easily affected by erosion.

Diagnosis – OL: OH = 1.35–1.4. Sulcus moderately narrow, shallow, with anteriorly widened ostium and posteriorly widened cauda. Colliculi fused, somewhat narrowed at collum, level with smooth inner face. Predorsal projection broad, gently rounded, slightly anterior of middle of otolith; ventral rim shallow, regularly curved. All rims very thick.

Description – Otoliths moderately compressed, thick (OH: OT about 2.0) with broad, rounded predorsal projection, up to 4 mm length. Dorsal rim rather gently curved with broad predorsal lobe. Ventral rim smooth, gently curved, shallow. Anterior tip inferior, broadly rounded; posterior tip inferior, slightly less broadly rounded than anterior tip. Inner face markedly convex, very smooth, with feeble ventral furrow close to ventral rim of otolith, dorsally with shallow, indistinct and small depression. Sulcus long, narrow, shallow, with median position, reaching close to anterior tip of otolith and terminating also close to posterior tip of otolith. Colliculi fused, smooth and level with inner face; ostium and cauda differentiated by a broad incursion of its ventral margin; dorsal sulcus margin regularly curved, convex. Ostium and rear portion of cauda slightly widened. Outer face concave, sometimes with pronounced tubercles near anterior and posterior tips and some rugose ornamentation at its center. All rims very thick.

Discussion – These otoliths are so characteristic in their appearance, amongst others due to their thick, cut rims, that they can easily be recognized even when strongly eroded. The overall shape of the otolith and its sulcus organization with the fused colliculi resembles the Recent *S. barbatus* (Meek and Hildebrand, 1928) (otolith investigated of specimen USNM 211,322), but differs in the shallow colliculi, the convex dorsal rim of the sulcus and the not projecting posterior tip.

Sanopus peregrinus n. sp. Aguilera and Schwarzhans

Fig. 7.4–7.7

Type material – Holotype, MPEG-1910-V (Fig. 7.4), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1911-V, four specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From peregrinus (Latin) = foreign, expatriate, referring to the disjunctive location of the species in respect to its Recent congeners found in reef environments of the central Caribbean.

Diagnosis – OL: OH = 1.1. Sulcus narrow, with a tapering tip and a rounded ostium. Colliculi fused, ridge-like elevated, slightly depressed at collum. Predorsal projection broad, massive, slightly anterior of middle of otolith; ventral rim shallow, regularly curved.

Description – Otoliths highly bodied, with very pronounced and broad predorsal projection, moderately thick (OH: OT = 2.2–2.5) and rather small, up to 2 mm length. Dorsal rim skewed triangular in shape, smooth posteriorly, slightly undulating and steeper anteriorly. Ventral rim smooth, gently curved, shallow. Anterior tip inferior, broadly rounded; posterior tip inferior, less broadly rounded than anterior tip. Inner face mildly convex, ventrally smooth, with ventral furrow close to ventral rim of otolith, dorsally with large and rather deep depression. Sulcus long, narrow, with median position, reaching close to anterior tip of otolith and terminating also not far from posterior tip of otolith. Colliculi fused; ostium and cauda differentiated by an indistinct incursion of its dorsal margin and a narrowing and slight depression of the joint and elevated colliculum. Ostium slightly widened; cauda slightly swinging, less widened, tapering. Outer face flat, smooth.

Discussion – These otoliths show an unmistakable outline and sulcus organization that resembles the one of the Recent *S. barbatus* (Meek and Hildebrand, 1928), but readily distinguishes in the high, triangular shape and the unusual fused and elevated colliculi. It is possible that these otoliths represent an extinct batrachoid genus.

Thalassophryne Günther, 1861

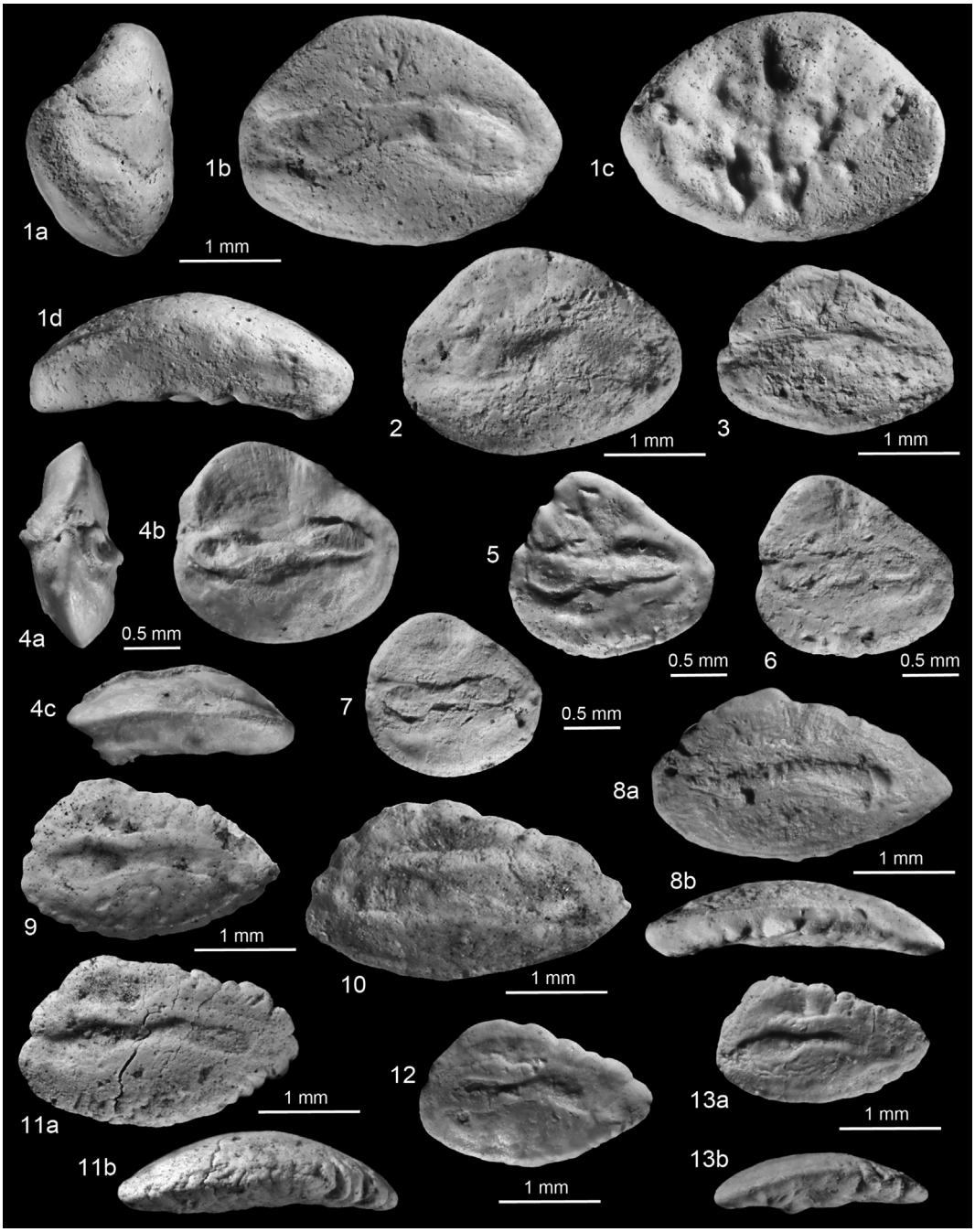

Fig. 7. 1 †*Sanopus mendax* n. sp., Holotype, MPEG-1938-V; 2–3 †*Sanopus mendax* n. sp., Paratypes, MPEG-1939-V; 4 †*Sanopus peregrinus* n. sp., Holotype, MPEG-1910-V; 5–7 †*Sanopus peregrinus* n. sp., Paratypes, MPEG-1911-V; 8 †*Thalassophryne aequaliter* n. sp., Holotype, MPEG-1822-V; 9–13 †*Thalassophryne aequaliter* n. sp. Paratype, MPEG-1918-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

Thalassophryne aequaliter n. sp. Aguilera and Schwarzhans
Fig. 7.8–7.13

Type material – Holotype, MPEG-1822-V (Fig. 7.8), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1918-V, eight specimens, same data as holotype.

Further material – MPEG-1941-V, six specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From aequaliter (Latin) = evenly, referring to the intermediate position of the otolith morphology.

Diagnosis – OL: OH = 1.6–1.8, increasing with size; CcL: OcL = 1.3–1.6. Dorsal rim moderately shallow, crenulated, with broad, weakly developed predorsal lobe; ventral rim shallow and crenulated; posterior tip pointed, inferior. Sulcus with separated colliculi; cauda slightly bent and widened posteriorly.

Description – Otoliths moderately thin (OH: OT = 2.2–2.7), elongate otoliths up to 3.2 mm length. OL: OH increasing with size from 1.6 at 2 mm length to 1.8 at 3 mm length. Dorsal rim rather shallow, regularly curved with broad predorsal projection and

intensely crenulated. Ventral rim shallow, gently curving, delicately crenulated or slightly undulating. Anterior tip rounded, inferior; posterior tip pointed, inferior. Inner face moderately bent. Sulcus nearly median, moderately shallow, long, terminating close to anterior and posterior rims of otolith. Ostium and cauda well distinguished with collum narrowed from dorsal and ventral and rather widely separated colliculi. Cauda about 1.5 times as long as ostium, slightly widened posteriorly and with slightly inclined dorsal margin. Dorsal depression long, moderately narrow, ventrally distinctly separated from sulcus by moderately wide crista superior. Ventral furrow mostly distinct, long, close to ventral rim of otolith. Outer face slightly concave to flat and with some marginal ornamentation.

Discussion — *Thalassophryne aequaliter* differs from all known otoliths of Recent species of the genus in being more elongate (except *T. nattereri* Steindachner 1876), the presence of a predorsal lobe, although weak, except for the presence of a more centrally positioned dorsal lobe in *T. megalops* Bean and Weed, 1910, while other Recent species show a depressed predorsal region. Also the cauda is less bent and longer than in the Recent species, resulting in

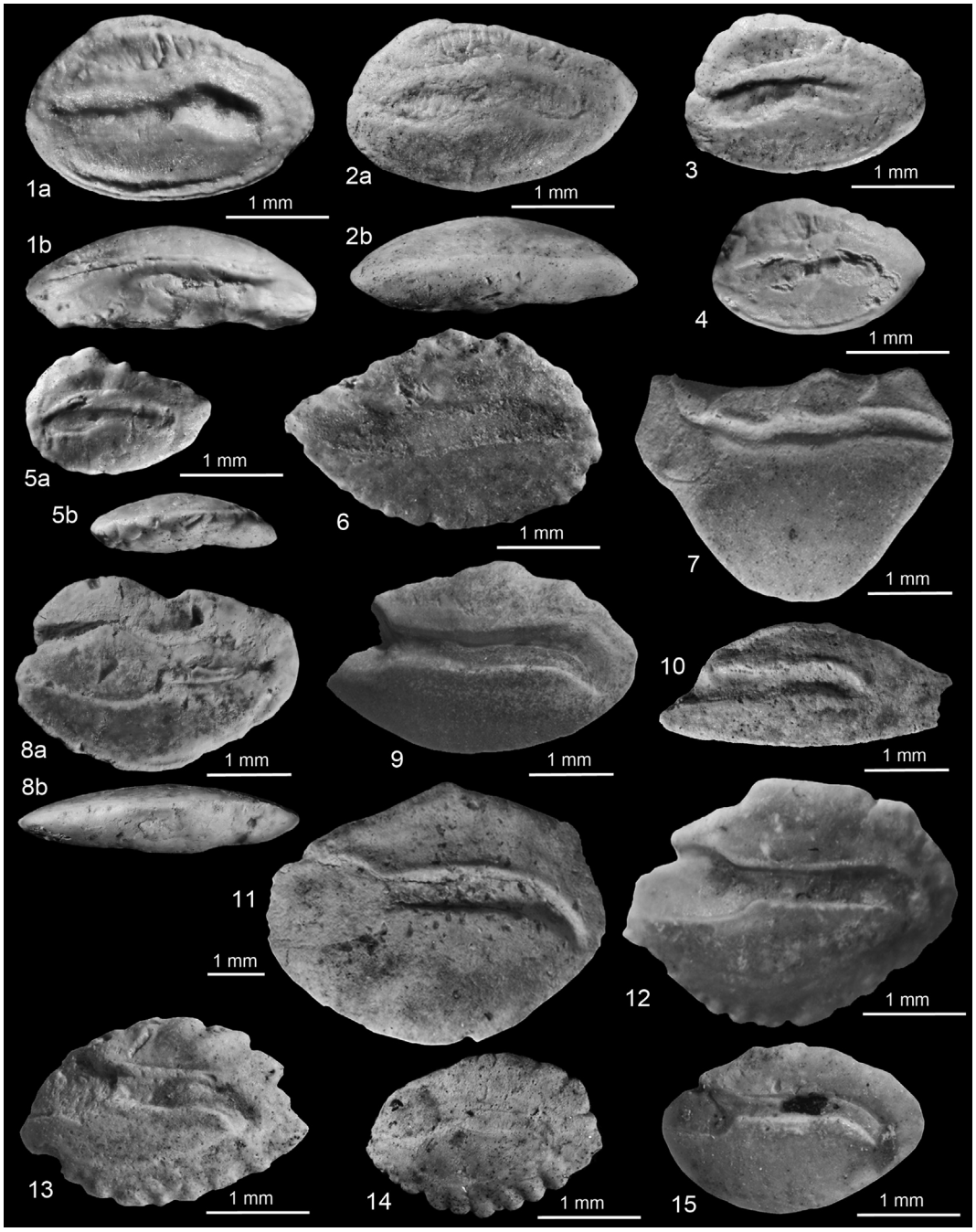

Fig. 8. 1 †*Thalassophryne pumilus* n. sp., Holotype, MPEG-1942-V; 2–5 †*Thalassophryne pumilus* n. sp., Paratypes, MPEG-1943-V; 6 *Hyporhamphus* sp., MPEG-1909-V; 7 *Ostichthys* sp., MPEG-1831-V; 8 *Apogon* sp., MPEG-1789-V; 9 *Decapterus* sp.; MPEG-1921-V; 10 Scorpaenidae Genera and species indet., MPEG-1920-V; 11 *Pristipomoides* sp., MPEG-1790-V; 12 *Archosargus* sp., MPEG-1791-V; 13–14 *Diapterus* sp., MPEG-1826-V; 15 *Ocyurus* sp., MPEG-1922-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

a distinctly plesiomorphic appearance of *T. aequaliter*. Another undescribed species of *Thalassophryne* has been figured from various Early to Middle Miocene strata of Trinidad by Nolf (1976), which is similarly elongate, but shows a depressed predorsal rim and the typical short and bent cauda.

Thalassophryne pumilus n. sp. Aguilera and Schwarzhans
Fig. 8.1–8.5

Type material – Holotype, MPEG-1942-V (Fig. 8.1), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1943-V, six specimens, same data as holotype.

Further material – MPEG-1944-V, 14 specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From pumilus (Latin) = dwarf, referring to the small, compact size of the otolith.

Diagnosis – OL: OH = 1.45–1.65; CcL: OcL = 0.8–1.0. Dorsal rim moderately shallow, with broad, weakly developed predorsal lobe; ventral rim shallow; posterior tip rounded or slightly pointed, inferior. Sulcus with separated, equally sized colliculi; cauda slightly bent and widened posteriorly.

Description – Otoliths moderately thick (OH: OT = 1.8–2.3, decreasing with size), compact otoliths up to 2.5 mm length. Dorsal rim rather shallow, regularly curved with broad predorsal projection, crenulated in specimens below 2 mm length. Ventral rim shallow, gently curving, smooth. Anterior tip rounded, inferior; posterior tip rounded, slightly projecting, inferior.

Inner face distinctly bent. Sulcus slightly supramedian, moderately deep, long, terminating close to anterior rim and at some distance from posterior rim of otolith. Ostium and cauda well distinguished with indention at collum only from ventral; dorsal rim of sulcus curved, convex, without marked indention at collum. Cauda about as long as ostium or slightly shorter, slightly widened posteriorly and with slightly inclined dorsal margin. Dorsal depression long, moderately narrow, ventrally distinctly separated from sulcus by moderately wide crista superior above ostium and collum. Ventral furrow mostly distinct, long, close to ventral rim of otolith. Outer face flat and rather smooth.

Discussion – The sulcus proportions with the equally long ostium and cauda and outline are more typical for the genus *Thalassophryne* than that of the parallel occurring *T. aequaliter*. The regular outline with the moderately developed predorsal lobe and the thick appearance distinguish *T. pumilus* from the otoliths of the Recent species known to the authors.

Hemirhamphidae
Hyporhamphus Gill, 1859
Hyporhamphus sp.
Fig. 8.6

Material – MPEG-1909-V, four otoliths, Atalaia Beach.

Discussion – One reasonably well preserved, thin, oval otolith of about 3 mm length with a convex inner and concave outer face. The anterior tip is pointed, the posterior rim broadly rounded and the dorsal and ventral rims gently curving. All rims are intensely crenulated. The sulcus is typical for hemirhamphids with ostium and cauda poorly distinguished, the ostium slightly dorsally widened as compared to the cauda and anteriorly almost closed and filled with a single colliculum.

Holocentridae
Ostichthys Cuvier in Cuvier and Valenciennes, 1829
Ostichthys sp.
Fig. 8.7

Material – MPEG-1831-V, two otoliths, Atalaia Beach.

Description – Compressed, high-bodied otoliths up to about 3.7 mm length. OL: OH = 1.35. Outline typical myripristin with very deep, regularly curved ventral rim, dorsally shifted anterior and posterior tips and flat, horizontal dorsal rim with rear part of dorsal depression of it inner face expending over it slightly behind middle of dorsal rim. Inner face slightly convex, with very wide and large, smooth ventral field. Sulcus extremely supramedian positioned, typical myripristin with short, ventrally expanded ostium and long, narrow, slightly swung cauda. Dorsal depression well marked in mid-dorsal position. Crista of dorsal depression developed at its dorsal and posterior margins. Outer face slightly convex and smooth.

Discussion – A well-preserved, typical otolith of the genus *Ostichthys* that differs from those of the genus *Myripristis* by the lack of a dorsal expansion of the ostium. Due to the still limited knowledge of Recent myripristin otoliths we have refrained from establishing of a new fossil species.

Scorpaenidae
Genera and species indet.
Fig. 8.10

Material – MPEG-1920-V, three eroded otoliths up to about 3.5 mm length, Atalaia Beach.

Discussion – Poorly preserved and eroded otoliths, which cannot be further identified.

Apogonidae
Apogon Lacepède, 1801
Apogon sp.
Fig. 8.8

Material – MPEG-1789-V, 13 eroded and/or juvenile otoliths, Atalaia Beach, which cannot be further identified.

Discussion – Poorly preserved and eroded otoliths, which cannot be further identified.

Carangidae
Decapterus Bleeker, 1851
Decapterus sp.
Fig. 8.9

Material – MPEG-1921-V, Atalaia Beach.

Discussion – Poorly preserved and eroded otolith, which cannot be further identified.

Lutjanidae
Pristipomoides Bleeker, 1852
Pristipomoides sp.
Fig. 8.11

Material – MPEG-1790-V, three otoliths, Atalaia Beach.

Description – Moderately well preserved and moderately thick otoliths up to 6 mm length. OL: OH = 1.3. Dorsal rim straight inclined anteriorly up to a sharp mediodorsal angle, thereafter straight, inclined backwards, but less so than anteriorly towards an obtuse postdorsal angle. Ventral rim deep and very regularly curved. Anterior tip with broadly rounded rostrum, but without antirostrum or excisura; posterior rim oblique with obtuse median angle behind tip of cauda. Inner face convex with distinctly supramedian sulcus. Sulcus divided into a broad, short, shallow, anteriorly widening ostium and a deeper, narrow, posteriorly markedly bent cauda terminating close to posterior tip of otolith. CcL: OcL = 1.65. Dorsal depression large, with moderately developed crista superior over ostium and anterior part of cauda. No ventral furrow. Outer face concave, smooth.

Discussion – Otoliths are known from two of the three Recent species in the tropical western Atlantic – *P. aquilonaris* (Goode and Bean, 1896) and *P. macrophthalmus* (Müller and Troschel, 1848) –

both of which exhibit a stronger ornamentation of the dorsal rim, a less strongly bent caudal tip and a well defined ventral furrow. The lack of a visible ventral furrow in our fossil specimens, however, could also be due to the moderate preservation, due to which we have refrained from establishing a new fossil species.

Ocyurus Gill, 1862
Ocyurus sp.
Fig. 8.15
Material – MPEG-1922-V, seven otoliths, Atalaia Beach.
Discussion – Poorly preserved, eroded juvenile otoliths, which cannot be further identified.

Gerreidae
Diapterus Ranzani, 1842
Diapterus sp.
Fig. 8.13–8.14
Material – MPEG-1826-V, five otoliths, Atalaia Beach.
Description – Small, oval and moderately thick otoliths up to about 2.8 mm length. OL: OH = 1.4–1.5. Dorsal regularly curved, posteriorly pronounced, with intense and coarse crenulation. Ventral rim regularly curved and intensely crenulated, but less strong and more regular than dorsal rim. Anterior tip obtuse, with bluntly rounded rostrum and no antirostrum or excisura; posterior tip ventrally projecting, moderately pointed. Inner face convex with supramedian and slightly inclined sulcus. Sulcus divided into a broad, short, somewhat deepened, anteriorly widening ostium and a narrow, posteriorly somewhat bent and deepened cauda terminating moderately close to posterior tip of otolith. CcL: OcL = 1.7. Dorsal depression short, only above anterior part of cauda, with distinct crista superior. Distinct ventral furrow positioned at considerable distance rim ventral rim of otolith. Outer face concave, intensely ornamented.
Discussion – The intense crenulation of the rims, the short rostrum and the posteriorly pronounced dorsal rim distinguish these otoliths from the Recent *Diapterus* species of the tropical West Atlantic. Due to the poor preservation of the otoliths available, we have refrained from establishing a new fossil species.

Sparidae
Archosargus Gill, 1865
Archosargus sp.
Fig. 8.12
Material – MPEG-1791-V, two otoliths of about 3 mm length, Atalaia Beach, which are considered.
Discussion – Juvenile otolith and too small to allow specific identification.

Sciaenidae
The diversity observed in sciaenid otoliths is amongst the most striking found in teleosts and has been subject to several detailed investigations, the most comprehensive being by Schwarzhans (1993). Terminology and morphometrics used here follow Schwarzhans (1993) and Bearez and Schwarzhans (2013).

Aplodinotus Rafinesque, 1819
†*Aplodinotus santosi* n. sp. Aguilera and Schwarzhans
Fig. 9.1–9.5
Type material – Holotype, MPEG-1792-V (Fig. 9.1), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1793-V, six specimens, same data as holotype.
Further material – MPEG-1794-V, 37 specimens, same data as type specimens.
Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.
Etymology – Named in honor of Rubens da Silva Santos, for his contributions to the knowledge of the Brazilian fossil fish fauna.
Diagnosis – OL: OH = 1.05–1.15. Ostium very large, about as wide as long. Cauda strongly bent downwards; posterior tip pointed with dorsally expanded margin reaching very close to posterior rim of otolith. Caudal curvature index about 0.7. Outer face mildly convex without umbo.
Description – Compressed, roundish, moderately thick otoliths up to about 5.5 mm length. OH: OT about 2.5. Dorsal rim shallow, nearly flat, slightly undulating; anterior, ventral and posterior rims deeply, regularly and continuously curving, except for nearly straight and slightly inclined upper section of posterior rim. Inner face moderately convex with distinctly supramedian sulcus. Sulcus divided into a shallow, extremely wide ostium and a strongly bent, narrow and deepened cauda. Ostium regularly shaped, about as wide as long, its rear margin slightly inclined towards anterior-dorsal, filled with shallow colliculum exhibiting clear precaudal depression. Cauda shorter than ostium (OcL: CcL = 1.3–1.4), its downward bent rear part extending slightly below ventral reach of ostium and slightly bent forward towards its pointed tip. Rear-dorsal margin of cauda markedly expanded. Dorsal depression indistinct and narrow; no ventral furrow. Outer face mildly convex with little ornamentation.
Discussion – *Aplodinotus santosi* is now the third marine fossil species of the genus, which in the Recent is represented by a single freshwater species – *A. grunniens* Rafinesque, 1819, distributed in rivers of North and Central America which discharge into the Atlantic Ocean – the other two being *A. hoffmani* Nolf and Aguilera, 1998 and *A. longecaudatus* Nolf and Aguilera, 1998, both from the Cantaure Fm. of Burdigalian age from Venezuela. It resembles well those species, particularly *A. grunniens* and *A. hoffmani*, and is readily distinguished by the distinctive expansion of the rear-dorsal portion of the caudal tip and the compressed outline. *Aplodinotus longecaudatus* shows a similarly compressed outline, but differs in the somewhat downward inclined dorsal margin of the ostium and the more regularly curved cauda with a more forward inclined caudal tip.

Equetulus n. gen. Aguilera and Schwarzhans
Type species – *Equetulus amazonensis* n. sp.
Etymology – Derived from *Equetus* Rafinesque, 1815, the genus considered to be most closely related.
Diagnosis – A fossil otolith-based genus of the family Sciaenidae with the following combination of characters. Compressed otoliths with a ratio OL: OH of 1.0–1.3, moderately thick, without umbo on outer face. Predorsal lobe variably developed; inferior posterior tip often pointed. Ostium much reduced in size, 3 to 4 times shorter than cauda and narrow. Cauda very regularly bent at junction of horizontal with vertical stretch.
Discussion – The small ostium and the regularly curved cauda distinguish these otoliths from the living genera *Equetus* and *Pareques* Gill, 1876. All three genera are undoubtedly related and comprise the *Equetus* Otolith Group as defined in Schwarzhans (1993).
Species – *Equetulus amazonensis* n.sp., described in the following from the Early Miocene, Aquitanian of Brazil, *E. davidandrewi* Nolf and Aguilera, 1998 from the Early Miocene, Burdigalian of Venezuela and *E. fitchi* Schwarzhans, 1993 from the Early to Middle Miocene (Aquitanian to Serravallian) of Venezuela, Trinidad and Brazil.

†*Equetulus amazonensis* n. sp. Aguilera and Schwarzhans
Fig. 9.6–9.11
Type material – Holotype, MPEG-1796-V (Fig. 9.6), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′

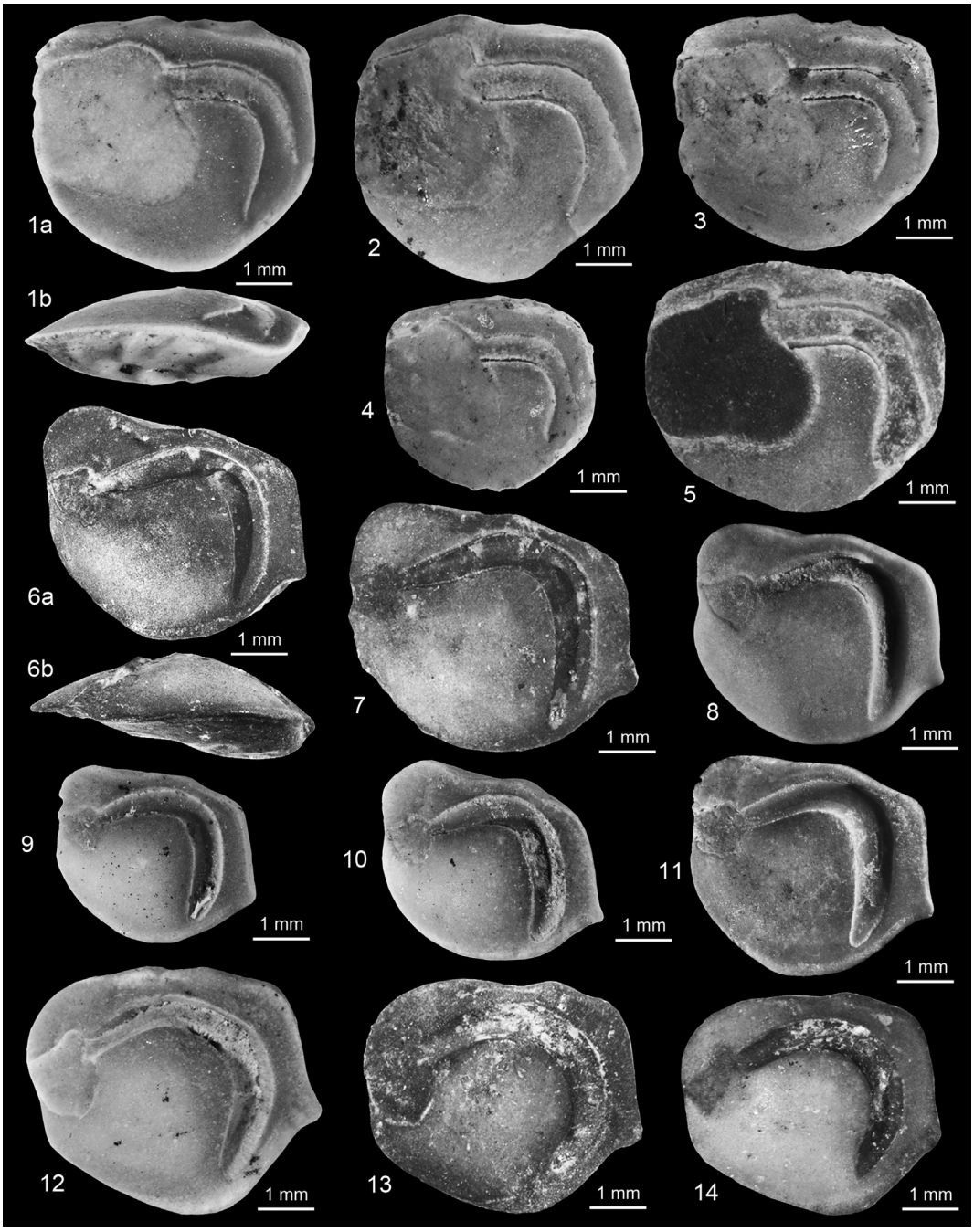

Fig. 9. 1 †*Aplodinotus santosi* n. sp., Holotype, MPEG-1792-V; 2–5 †*Aplodinotus santosi* n. sp., Paratypes, MPEG-1793-V; 6 †*Equetulus amazonensis* n. sp., Holotype, MPEG-1796-V; 7–11 †*Equetulus amazonensis* n. sp., Paratypes, MPEG-1797-V; 12 †*Equetulus fitchi*, MPEG-1799-V, 13–14 †*Equetulus fitchi*, MPEG-1800-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

55.6″ W); Paratypes, MPEG-1797-V, 17 specimens, same data as holotype.

Further material – MPEG-1798-V, 715 specimens, same data as type specimens.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Named after the Amazon River, which discharges into the South Atlantic near the outcrops of the type locality.

Diagnosis – OL: OH = 1.05–1.15. Strong, anterior-dorsally projecting predorsal lobe. Inferior short, but well marked pointed tip at posterior rim. Ostium very small, about ¼ the length of cauda and not much wider than cauda at its largest width. Faint ventral furrow present near central portion of ventral field close to ventral rim of otolith leading to tip of cauda.

Description – Compressed, moderately thick otoliths up to 5.5 mm length, with somewhat parallelogram-shaped outline due to strongly projecting anterior-dorsal lobe and presence of distinct inferior posterior tip. OH: OT about 2.5. Dorsal rim straight, inclined backwards from anterior-dorsal projection; anterior and ventral rims regularly and continuously curving; posterior rim upward-anteriorly inclined above inferior tip and

joint to dorsal rim in gentle curve. Inner face moderately convex with distinctly supramedian sulcus. Ostium extremely small as compared to cauda, shallow, sometimes with reduced opening, slightly bent downwards. Cauda long, steeply curving in a regular bent; its vertical section reaching close to posterior-ventral rim with pointed tip. Cauda somewhat deepened and reaching its greatest width within the maximally bent region. Dorsal depression minute, indistinct; ventral furrow feeble, recognizable along narrow stretch close to mid-ventral rim and connecting to tip of cauda. Outer face slightly convex posteriorly and flat anteriorly, smooth.

Discussion – Otoliths of *E. amazonensis* are readily recognized by their minute ostium, the strongly expanded anterior-dorsal projection and the inferior pointed posterior tip.

†*Equetulus fitchi* (Schwarzhans, 1993)
Fig. 9.12–9.14

1976 genus aff. *Pachypops* sp. – Nolf: pl.8, figs. 4–5
1993 *Pachypops fitchi* – Schwarzhans: figs. 115–18

Material – MPEG-1799-V, 193 otoliths; MPEG-1800-V, 47 otoliths, Atalaia Beach.

Description – Compressed, rounded otoliths up to nearly 8 mm length. Predorsal lobe depressed; ventral rim with deepest point below caudal tip; posterior rim with slightly inferior moderately pointed tip. Inner face slightly convex with distinctly supramedian sulcus. Ostium small, less than half the length of cauda, distinctly declined, with much reduced opening. Cauda very regularly half-moon shaped with its pointed tip distinctly bent forward. Indistinct dorsal depression; no ventral furrow. Outer face flat to slightly convex, smooth.

Discussion – *Equetulus fitchi* is a common and widely distributed species in the Early and Middle Miocene from Venezuela to Brazil. Originally placed in the freshwater genus *Pachypops* by Nolf (1976) and Schwarzhans (1993), its sulcus organization now has lead to rearrangement with the new fossil genus *Equetulus*. Size and shape of the ostium, lack of a pronounced predorsal lobe and the regular curvature of the cauda easily distinguish *E. fitchi* from the contemporaneous *E. amazonensis*.

Protolarimus n.gen. Aguilera and Schwarzhans

Type species – *Larimus henrici* Nolf and Aguilera, 1998

Etymology – Referring to the plesiomorphic morphology related to the genus *Larimus* Cuvier, 1830.

Diagnosis – A fossil otolith-based genus of the family Sciaenidae with the following combination of characters. Moderately elongated otoliths with a ratio OL: OH of 1.4–2.0, moderately thick, without umbo on outer face. Predorsal lobe angular, not elevated; ventral rim almost straight. Ostium inclined with sinuate dorsal margin and anteriorly opened, postostial lobe not much expanded. Cauda strongly bent, reaching beyond level of ventral margin of ostium.

Discussion – The particular shape of the anteriorly open ostium with its sinuate upper margin ostium and the outline of the otolith with the shallow predorsal lobe and the straight ventral rim as well as the rather wide space between ostium and the downturned part of the cauda distinguish *Protolarimus* from the extant *Larimus*, which is also recorded since Early Miocene times. *Protolarimus* is interpreted as the plesiomorphic member of the *Larimus* Otolith Group as defined in Schwarzhans (1993).

Species – *Protolarimus mauryae* n. sp., described in the following from the Early Miocene, Aquitanian of Brazil and *P. henrici* Nolf and Aguilera, 1998 from the Early Miocene (Burdigalian) of Venezuela.

†*Protolarimus mauryae* n. sp. Aguilera and Schwarzhans
Fig. 10.1–10.2

Type material – Holotype, MPEG-1805-V (Fig. 10.1), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1806-V, three specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Named in honor of Carlotta Joaquina Maury, in recognition of her contributions to the knowledge of the Pirabas Formation.

Diagnosis – OL: OH = 1.4–1.5. Ostium inclined, dorsally much inflected, sinuate. Outline almost rectangular. Predorsal region slightly elevated, angularly set-off from inner face along edge. Caudal curvature index = 0.8.

Description – Compact, robust, moderately thick otoliths up to 6 mm length. OH: OT = 1.7. Outline almost rectangular, slightly wider anteriorly than posterior. Predorsal lobe shallow; dorsal and ventral rims rather flat; anterior rim blunt, posterior rim nearly vertically cut. Inner face markedly convex with supramedian sulcus. Ostium moderately large, shallow, distinctly inclined, with sinuate inflected dorsal margin and little postostial lobe, anteriorly open, about as long as cauda. Cauda strongly bent, its vertical portion slightly widened and slightly bent forward at its tip. Dorsal field with no distinct depression, but edge above ostium setting off the portion of inner face extending into shallow predorsal lobe; no ventral furrow. Outer face moderately convex, rather smooth.

Discussion – *Protolarimus mauryae* differs from the slightly younger *P. henrici* from Venezuela in the more compressed shape (OL: OH = 1.4–1.5 vs 2.0) and the less expanded postostial lobe.

Pachyurus Agassiz, in Spix and Agassiz, 1831

†*Pachyurus jungi* Aguilera and Rodrigues de Aguilera, 2004
Fig. 10.3

2004 *Pachyurus jungi* – Aguilera and Rodrigues de Aguilera: pl.1, figs. 13–16

Material – MPEG-1807-V, 26 otoliths, Atalaia Beach.

Description – Moderately compressed, oval otoliths up to about 7.5 mm length. Predorsal lobe moderately developed, somewhat projecting anteriorly; dorsal rim rather flat, smooth; ventral rim shallow, smooth, regularly curved; anterior and posterior rims broadly rounded.

Inner face markedly convex with distinctly supramedian sulcus. Ostium large, equal in length to cauda, somewhat bent downwards towards anterior. Cauda very regularly half-moon shaped with its pointed tip distinctly bent forward, leaving very little space on inner face towards posterior rim. Indistinct, narrow dorsal depression; no ventral furrow. Outer face convex, with postcentral umbo and sometimes with broad tubercles.

Discussion – *Pachyurus jungi* was originally described from the slightly younger Cantaure Fm. of Venezuela, but was not identified from Trinidad.

Plagioscion Gill, 1862

†*Plagioscion marinus* Aguilera and Rodrigues de Aguilera, 2003
Fig. 10.9–10.11

2003 *Plagioscion marinus* – Aguilera and Rodrigues de Aguilera: figs. 4.1–4.4

Material – MPEG-1801-V, 13 otoliths; MPEG-1802-V, 37 otoliths, Atalaia Beach.

Description – Large, moderately compressed, subrectangular otoliths up to nearly 15 mm length. OL: OH = 1.35–1.55. Dorsal rim rather shallow, highest at its middle, slightly inclined anteriorly; ventral rim much deeper, deepest behind middle below tip of cauda; anterior rim almost straight, inclined, with the most projecting point at upper margin of ostium; posterior blunt, broad, with cut, slightly dorsally inclined rim and oblique upper and lower

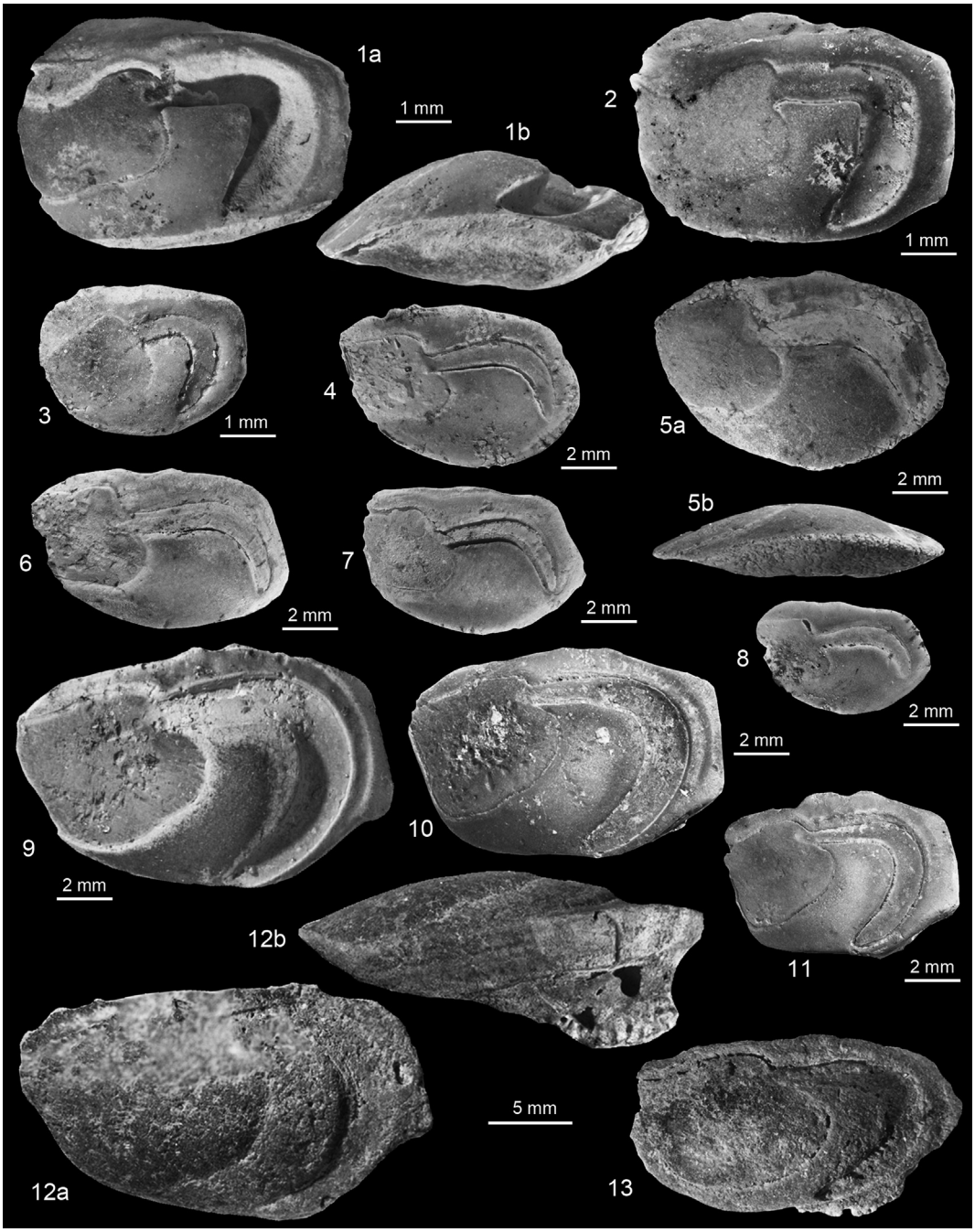

Fig. 10. 1 †*Protolarimus mauryae* n. sp., Holotype, MPEG-1805-V; 2 †*Protolarimus mauryae* n. sp., Paratypes, MPEG-1806-V; 3 †*Pachyurus jungi*, MPEG-1807-V; 5 †*Sciaenops rossettiae* n. sp., Holotype, MPEG-1808-V; 4, 6–8 †*Sciaenops rossettiae* n. sp., Paratypes, MPEG-1809-V; 9 †*Plagioscion marinus*, MPEG-1801-V, 10–11 †*Plagioscion marinus*, MPEG-1802-V; 12 †*Plagioscion travassosi* n. sp., Holotype, MPEG-1803-V; 13 †*Plagioscion travassosi* n. sp., Paratypes, MPEG-1804-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

angles, the lower angle being slightly stronger developed. Inner face moderately convex with distinctly supramedian sulcus. Ostium large, slightly bent downwards and widening towards anterior; postostial lobe weak. Cauda regularly half-moon shaped with its pointed tip distinctly bent forward for almost entire length, leaving little space on inner face towards posterior rim. Indistinct, narrow dorsal depression; no ventral furrow. Outer face convex, with postcentral umbo and some broad tubercles.

Discussion – In the Recent, fishes of the genus *Plagioscion* are adapted to freshwater and migrating into brackish water at times. Its otoliths are easily recognized by the specific shape of the outline of the otolith, the shape of the ostium and the cauda being bent forward at its tip to nearly its entire length. Therefore, *P. marinus* and the new species described in the following demonstrate their parallel occurrence in marine strata during the Miocene.

†*Plagioscion travassosi* n. sp. Aguilera and Schwarzhans
Fig. 10.12–10.13

Type material – Holotype, MPEG-1803-V (Fig. 10.12), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47°

18′ 55.6″ W); Paratypes, MPEG-1804-V, two specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Named in honor of Haroldo Travassos, for his contributions to knowledge of Brazilian fossil fishes.

Diagnosis – OL: OH = 1.7–1.8. Dorsal rim shallow, nearly straight. Anterior rim strongly inclined ventrally to join ventral rim without angle. Posterior rim reduced to about half the maximum height of otolith; its ventral angle somewhat projecting.

Description – Very large, moderately elongate otoliths up to about 25 mm length. OH: OT about 1.4. Dorsal rim shallow, nearly flat, not inclined anteriorly; ventral rim rather deep, deepest behind middle below tip of cauda, rather regularly curved, anteriorly continuously joined with the strongly posterior-ventrally inclined anterior rim; posterior blunt, about half the height of otolith, with slightly dorsally inclined rim, well rounded upper angle and somewhat projecting lower angle.

Inner face moderately convex with distinctly supramedian sulcus. Ostium large, very slightly bent downwards and widening towards anterior; postostial lobe weak. Cauda regularly half-moon shaped with its pointed tip distinctly bent forward for entire length, leaving little space on inner face towards posterior rim. Indistinct, narrow dorsal depression; no ventral furrow. Outer face strongly convex, with thick postcentral umbo.

Discussion – *Plagioscion travassosi* represents the third fossil marine species of the genus, being distinguished from the other two (*P. marinus* Aguilera and Rodrigues de Aguilera, 2003 and *P. urumacoensis* Aguilera and Rodrigues de Aguilera, 2003) by their more elongate shape, the flat dorsal rim and the not so much downward bent ostium. It is also more elongate than any of the known Recent species, with the one resembling closest being *P. squamosissimus* (Heckel, 1840) from the Amazonas River scheme.

Protosciaena Sasaki, 1989

†*Protosciaena brasiliensis* n. sp. Aguilera and Schwarzhans

Fig. 11.1–11.7

Type material – Holotype, MPEG-1816-V (Fig. 11.2), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1817-V, six specimens, same data as holotype.

Further material – MPEG-1818-V, 30 specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Referring to Brazil, as the country from which the species is being described.

Diagnosis – OL: OH = 1.05–1.1. Dorsal rim shallow, ventral rim deeply curved. Rear margin of ostium inclined. Caudal tip rounded but not or only weakly widened.

Description – Very compressed, high bodied otoliths up to about 7 mm length. OH:OT about 2.0. Dorsal rim shallow, anteriorly straight, posteriorly inclined behind a marked obtuse postdorsal angle located above bend of cauda; ventral rim very deep, regularly curved, smooth; anterior rim broadly rounded, nearly vertical, slightly projecting above upper ostial margin; posterior rim with obtuse angle at about tip of cauda. Inner face markedly convex with distinctly supramedian sulcus. Ostium large, ventrally much expanded, narrowing towards anterior, its rear margin inclined anterior-dorsally/posterior-ventrally. Cauda curved at somewhat less than 90° with near vertical section slightly shorter than horizontal section resulting in caudal curvature index of about 1.5; caudal tip rounded, not or very slightly widened. Dorsal depression narrow; no ventral furrow.

Outer face uniformly convex, without distinct umbo, smooth.

Discussion – *Protosciaena brasiliensis* represents the second fossil species of the genus along with *P. neritica* Aguilera and Rodrigues de Aguilera, 2004. Both are distinguished from the Recent *P. trewavasae* by the lack of a widened tadpole-like caudal tip. The high-bodied outline with the deep ventral rim and the specific shape of the ostium distinguish *P. brasiliensis* from the other two species.

Sciaenops Gill, 1864

†*Sciaenops rossettiae* n. sp. Aguilera and Schwarzhans

Fig. 10.4–10.8

Type material – Holotype, MPEG-1808-V (Fig. 10.5), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1809-V, four specimens, same data as holotype; further specimens, MPEG-1810-V, nine specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – Named in honor of Dilce de Fátima Rossetti, in recognition of her contributions to the knowledge of Brazilian geology.

Diagnosis – OL: OH = 1.45–1.6; OH: OT about 3.0. Dorsal rim shallow, ventral rim regularly curved. Anterior and posterior rims parallel inclined resulting in a parallelogram shaped otolith outline. Ostium shorter than cauda; OcL: CcL = 0.8. Cauda bent in less than 90°; caudal curvature index about 1.2.

Description – Oval shaped, rather thin otoliths up to about 10 mm length. Dorsal rim shallow, slightly and regularly curved without angles except for obtuse, rounded postdorsal angle located slightly behind bent of cauda; ventral rim deep, very regularly curved, smooth; anterior rim distinctly anterior-ventrally inclined, slightly projecting above upper ostial margin; posterior rim posterior-dorsally inclined with obtuse tip slightly above tip of cauda. Inner face moderately convex with distinctly supramedian sulcus. Ostium moderately large, not inclined, with moderate postostial lobe. Cauda curved at less than 90° with relatively short inclined section and low caudal curvature index of about 1.5; caudal tip pointed. Dorsal depression narrow, small; no ventral furrow. Outer face flat to slightly convex, less convex than inner face, smooth.

Discussion – *Sciaenops rossettiae* differs from the Recent *S. ocellatus* (Linnaeus 1766) and the fossil *S. reyesi* Aguilera and Rodrigues de Aguilera, 2004 from the Cantaure Fm. of Venezuela in the parallelogram-like shape of the otolith, the relatively short ostium and the less than 90° bent cauda.

Umbrina Cuvier, 1817

Umbrina sp. 1

Fig. 12.1

Material – MPEG-1795-V, one otolith, Atalaia Beach.

Discussion – A single, relatively large otolith of about 7 mm length, which resembles otoliths of the genus *Umbrina* as well as *Sciaena* due to its very large ostium, but which cannot be further identified due to poor preservation.

Umbrina sp. 2

Fig. 12.2–12.4

Material – MPEG-1945-V, four otoliths, Atalaia Beach.

Discussion – These smaller otoliths of 3–4.6 mm length differ from the foregoing one in being more compressed and showing a considerably smaller ostium. They are too small for a sciaaenid of the genus *Umbrina* to warrant identification.

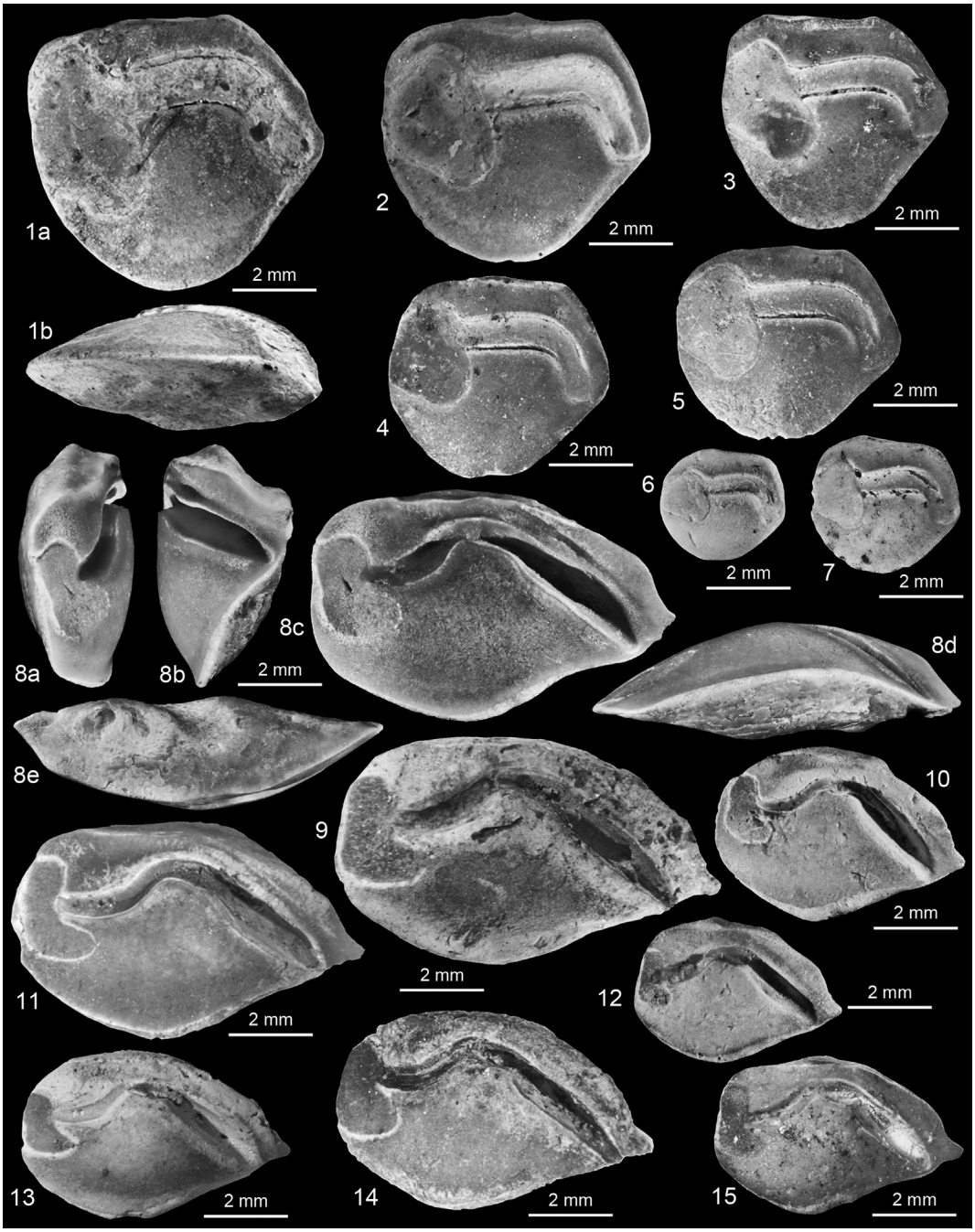

Fig. 11. 1, 3–7 †*Protosciaena brasiliensis* n. sp., Paratypes, MPEG-1817-V; 2 †*Protosciaena brasiliensis* n. sp., Holotype, MPEG-1816-V; 8 †*Xenotolithus retrolobatus* n. sp., Holotype, MPEG-1811-V; 9–15 †*Xenotolithus retrolobatus* n. sp., Paratypes, MPEG-1812-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

Xenotolithus Schwarzhans, 1993

†*Xenotolithus retrolobatus* n. sp. Aguilera and Schwarzhans
Fig. 11.8–11.15

Type material – Holotype, MPEG-1811-V (Fig. 11.8), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1812-V, 12 specimens, same data as holotype.

Further material – MPEG-1813-V, 167 specimens, same data as type material.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From retrus (Latin) = retro and lobatus (Latin) = lobed, referring to the well-developed postostial lobe.

Diagnosis – OL: OH = 1.5–1.7. Ostium with marked postostial lobe, ventrally expanding way beyond the ostial-caudal joint.

Description – Moderately elongate, rather thin otoliths up to about 10 mm length. Dorsal rim shallow anteriorly and gently curved, posteriorly considerably bending downwards; ventral rim deeper, regularly curved anteriorly, posteriorly almost straight ascending, smooth; anterior rim broadly rounded; posterior tip sharply pointed, shifted towards ventral. Inner face moderately convex with distinctly supramedian, very unusual sulcus. Ostium short and compressed, high, particularly ventrally, with well

developed distinctly backward extended postostial lobe. Cauda narrow and deepened, anterior portion concave, bending upward, then bedding downward in an obtuse angle of about 120–130° into a long, more deepened, straight, fusiform shaped, inclined longer stretch of cauda running parallel to posterior part of dorsal rim. Caudal curvature index about 0.65–0.75. Dorsal depression small, only above anterior, concave part of cauda; no ventral furrow. Outer face flat to slightly convex, smooth.

Discussion – When Nolf first recorded similar otoliths from the Early Miocene of Trinidad in 1976 as genus *Sciaenidarum* sp. and when Schwarzhans (1993) established the fossil otolith-based genus *Xenotolithus* for those specimens, there peculiar morphology was extensively discussed and it was not at all certain that they would really represent a sciaenid fish. Now the find of *X. retrolobatus* with the much postventrally extended ostial lobe supports indeed the view that these otoliths represent an extinct sciaenid with a highly apomorphic otolith morphology. *Xenotolithus retrolobatus* is considered as the oldest and most plesiomorphic member of this extinct group leading to *X. sasakii* Schwarzhans, 1993 in the slightly younger Miocene of Trinidad

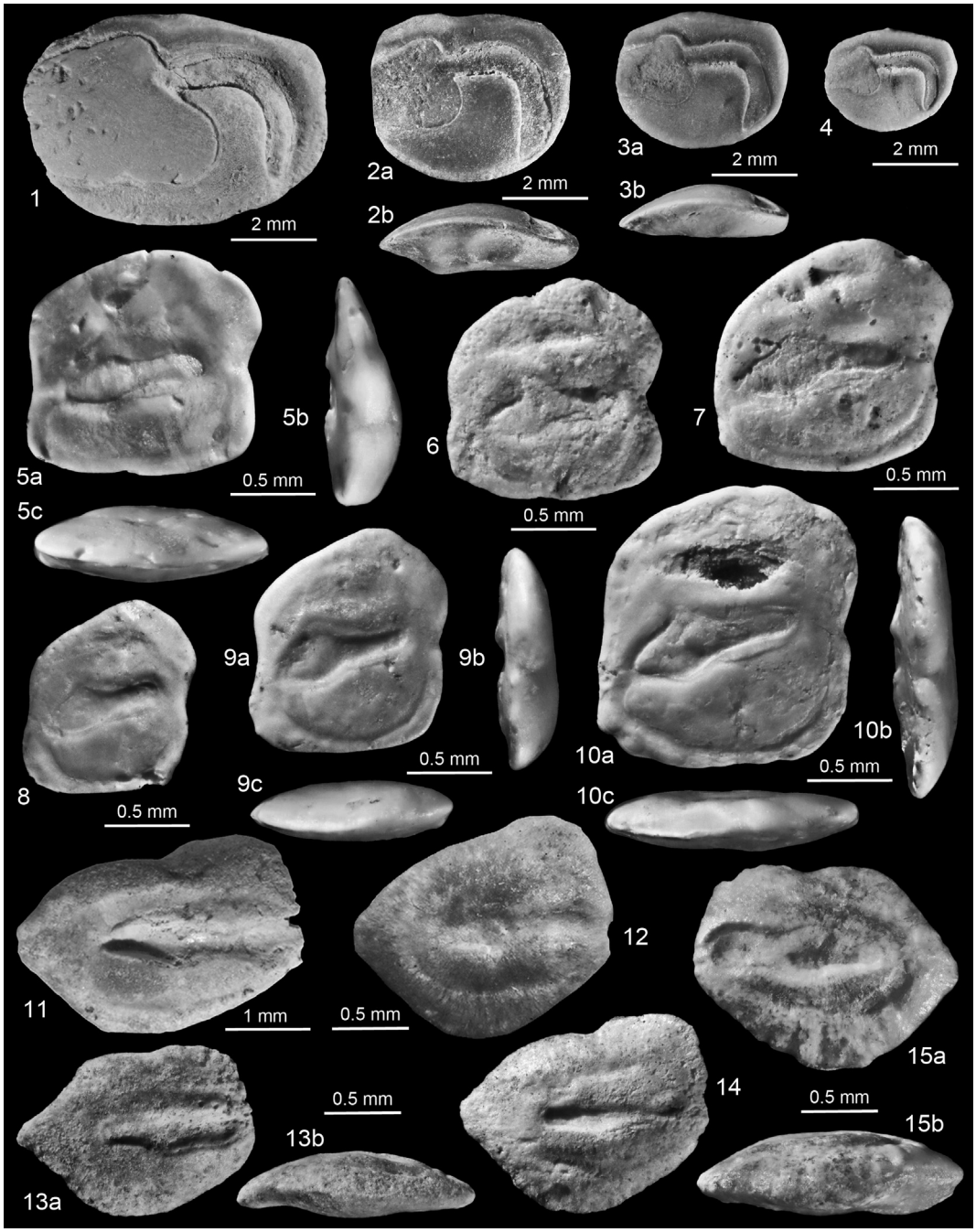

Fig. 12. 1 *Umbrina* sp. 1, MPEG-1795-V; 2–4 *Umbrina* sp. 2, MPEG-1945-V; 5–7 Gobiidae, Genera and species indet. 1, MPEG-1820-V; 8–9 Gobiidae, Genera and species indet. 2, MPEG-1946-V; 10 Gobiidae, Genera and species indet. 3, MPEG-1947-V; 11 *Cyclopsetta* sp., MPEG-1948-V; 14 †*Syacium predorsalis* n. sp., Holotype, left otolith, MPEG-1814-V; 12–13 †*Syacium predorsalis* n. sp., Paratypes, left otoliths, MPEG-1919-V; 15 †*Syacium predorsalis* n. sp., Paratype, right otolith, MPEG-1919-V. Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W).

with its extremely compressed sulcus without a postostial lobe and finally a further yet undescribed species with a totally reduced ventral portion of the ostium.

Gobiidae

Gobiid otoliths represent the most common near shore fishes found in practically all shallow water sediments of the Neogene, but are surprisingly rare at Atalaia Beach. The knowledge of Recent gobiids from South America is still very restricted and does not warrant identification of any of the morphologies identified.

Genera and species indet. 1

Fig. 12.5–12.7

Material – MPEG-1820-V; eight small, high bodied gobiid otoliths (OL: OH = 0.95–1.05) of unknown relation up to about 1.7 mm length from Atalaia Beach. They are characterized by a nearly rectangular outline with slightly projecting postdorsal lobe, which is not bend outwards.

Genera and species indet. 2

Fig. 12.8–12.9

Material – MPEG-1946-V; two small, very high bodied gobiid otoliths (OL: OH = 0.85) of unknown relation of about 1 mm length from Atalaia Beach. Apart from their compressed shape, these otoliths are further characterized by prominent postdorsal angle but no postdorsal lobe and a slight parallelogram like shift of the outline.

Genera and species indet. 3

Fig. 12.10

Material – MPEG-1947-V; a single small, high bodied gobiid otolith OL: OH = 0.9 of unknown relation of about 1.5 mm length from Atalaia Beach. This otolith is characterized by the almost perfectly rectangular outline with only the dorsal rim somewhat curved and its rather thin appearance.

Paralichthyidae

Cyclopsetta Gill, 1889

Cyclopsetta sp.

Fig. 12.11

Material – MPEG-1948-V, one otolith, Atalaia Beach.

Discussion – This single, well preserved otolith of about 3.6 mm length is characterized by a moderate elongate shape and a well developed predorsal lobe at the dorsal rim resembling the Recent *C. chittendeni* Bean, 1895 from the Caribbean and its allopatric counterpart *C. querna* (Jordan and Bollman, 1890) from the Pacific coast of Panama and Columbia.

Syacium Ranzani, 1842

Syacium predorsalis n. sp. Aguilera and Schwarzhans

Fig. 12.12–12.15

Type material – Holotype, MPEG-1814-V (Fig. 12.14), Atalaia Beach, Salinópolis Municipality, Pará State, Brazil (0° 35′ 33.6″ S, 47° 18′ 55.6″ W); Paratypes, MPEG-1919-V, 10 specimens, same data as holotype.

Locality and geological age – Early Miocene, Aquitanian, Pirabas Formation, Atalaia Beach, Salinópolis Municipality, Pará State, Brazil.

Etymology – From praedorsalis (Latin) = predorsal, referring to the much projecting predorsal lobe of the dorsal rim (in left otoliths).

Diagnosis – OL: OH = 1.2–1.4. Sulcus narrow in left otoliths (slightly wider in right otoliths) without much expanded anterior portion of cauda. Dorsal rim with strongly projecting predorsal lobe in left otoliths (less in right otoliths).

Description (of left otoliths) – Otoliths rhomboid shaped, thin, up to 2 mm length. Dorsal rim with very distinct, massive predorsal lobe at its beginning, thereafter almost straight, more or less regularly inclined downwards, sometimes with obtuse postdorsal angle; ventral rim deeply curved with a broad, rounded medioventral angle; anterior rim with broad, obtuse, rounded tip at about level of ostium; posterior tip pointed at or slightly below tip of cauda. All rims smooth or slightly undulating. Inner face slightly convex with nearly median positioned, slightly deepened and poorly structured sulcus. Ostium and cauda poorly separated; ostium shorter than cauda; anterior part of cauda only slightly widened; colliculi not separated. Dorsal depression wide, with indistinct margins; ventral depression narrow, underpinned by distinct furrow, positioned closer to sulcus than ventral rim of otolith, connected with dorsal depression behind caudal tip. Outer face flat to slightly concave, smooth.

Side dimorphism – Otoliths of many Pleuronectiformes are known to exhibit side dimorphism, obviously as a result of their asymmetrical head (Schwarzhans, 1999). In the case of *S. predorsalis* this is expressed in right otoliths (Fig. 12.15) exhibiting a slightly wider sulcus, a somewhat lees strongly developed predorsal lobe and in being thicker (OH: OT = 2.3 vs 2.6).

Discussion – Otoliths of *S. predorsalis* are distinguished from all Recent and fossil species of the genus by the distinct, massive predorsal lobe.

5. Faunal evaluation

5.1. Fish assemblages

The fossil otolith assemblages preserved in the Pirabas Fm. demonstrate a community dominated by shallow water coral reef-associated fishes. Taxa such as *Albula, Otophidium*, *Ogilbia, Ogilbichthys, Sanopus, Ocyurus, Archosargus* and *Hyporhamphus* all commonly occur in water shallower than 15 m close to or within reefs (Menezes et al., 2003; Froese and Pauly, 2014). Other taxa such as *Batrachoides*, *Carapus, Syacium*, *Sphyraena* and *Thalassophryne* are shallow-water dwellers that inhabit environments near reefs (Froese and Pauly, 2014). The genera *Ogilbia, Ogilbichthys* and *Sanopus* today only live in reefs in the Caribbean and do not extend southward to Brazil (Møller et al., 2004, 2005; Froese and Pauly, 2014).

Marine demersal fishes are represented by the genera *Paraconger, Pythonichthys, Amphiarius, Aspistor, Bagre, Cathorops* and *Porichthys* which are mainly bottom feeders that inhabit shallow water to about 50 m. *Pristipomoides*, *Protosciaena* and *Sciaenops* represent coastal demersal species that inhabit sandy or muddy bottoms (Froese and Pauly, 2014).

There is no evidence of ancestral marine sciaenid genera that are nowadays restricted to freshwater environments despite the occurrence of *Aplodinotus* and *Plagioscion* (Chao, 1978; Froese and Pauly, 2014). This is in line with the phylogenetic hypothesis of Cooke et al. (2011) who assumed a marine origin of the genus *Plagioscion* in South America. *Aplodinotus* is today restricted to freshwaters of North and Central America south of Guatemala, while *Plagioscion* is widely distributed genus in the rivers of South America with several species in the Amazon and Orinoco rivers (Cassatti, 2005).

Gobiidae are represented by rather few otoliths, which is remarkable considering that they usually dominate shallow near-shore and transitional marine environments. Epipelagic suspension-feeders such as clupeids and engraulids have not been found.

Species of the deeper shelf are few: *Ostichthys* with a benthopelagic habit from 150 to 400 m and *Paraconger,* at depths mostly around 50 m (Froese and Pauly, 2014). Oceanic midwater fishes of

the Myctophidae are entirely missing, while they are dominant in Neogene to Holocene sediments deposited below 200 m water depth (Schwarzhans, 2013). Their absence from the Pirabas Fm. is a clear shallow water indicator, while they are common in the lower Miocene rocks studied of Venezuela and Trinidad (Schwarzhans and Aguilera, 2013).

The fish fauna is in agreement with the paleoenvironmental analysis of the sediments of the Atalaia section, characterized by 1) fine-grained deposits with marls, claystones and siltstones representing low energy lagoon deposits, 2) very fine-grained sediments with greenish to dark gray shales deposited in a tidal flat environment, 3) carbonates with medium to coarse biocalcirudites and biocalcilutites deposited on the shallow upper platform. Therefore, our findings of the teleost fauna as reconstructed from otoliths assembalges support the theory that the Pirabas Fm. was deposited in a coastal, normal marine environment which may have been exposed to intense wave action, littoral currents, tropical coastal winds and storms as evidenced by the presence of reef-building calcareous algae, mollusks, corals, bryozoans, barnacles and echinoids.

Sciaenids (and batrachoidids) were particularly diverse and abundant in the Pirabas fish fauna like in other proto-Caribbean Neogene deposit. For instance †*Equetulus davidandrewi* (Nolf and Aguilera, 1998) and †*Plagioscion marinus* Aguilera and Rodrigues de Aguilera, 2004 were described from the lower Miocene Cantaure Fm. in Venezuela, and †*Equetulus fitchi* (Schwarzhans, 1993) from the upper Miocene Manzanilla Fm. of Trinidad. Remarkable is also the exceptional abundance of otoliths of †*Xenotolithus retrolobatus* n. sp. of the extinct genus †*Xenotolithus* first described from the upper Miocene Manzanilla Fm. of Trinidad (†*X. sasakii* Schwarzhans, 1993).

The complete sciaenid diversity of the Pirabas Fm. includes several new shallow water species, namely †*Aplodinotus santosi*, n. sp., †*Equetulus amazonensis* n. sp., †*Protolarimus mauryae* n. sp., †*Plagioscion travassosi* n. sp., †*Protosciaena brasiliensis* n. sp., † *Sciaenops rossettiae* n. sp. and †*Xenotolithus retrolobatus* n. sp.

5.2. Associated biota on the carbonate platform

The main carbonate producer of the calcareous deposits of the Pirabas Fm. is the coralline algae of the genera *Lithophyllum, Corallium* and *Lithothamnium* (Sommer, 1967). Reef-building corals were not recovered from the Atalaia section, but solitary azooxanthellitic corals are common and represented by the genera *Fabellum, Dendrophyllia, Balanophyllia, Cladocora, Discotrochus* and *Stylophora* (Maury, 1925; Fernandes, 1979, 1981). Bryozoans were described of the genera *Cupuladria*, *Lunulites* and *Steginoporella* (Maury, 1924; Barbosa, 1959a, b, 1957) including an undescribed *Discoporella* species from the Atalaia section. The biocalcirudites and biocalcilutites exhibit a high diversity of fossil mollusks (Maury, 1925), most of them are suspension and grazing feeders that live associated with seagrass environments and calcareous algae.

The carbonatic coquina contains a high frequency of regular and irregular echinoids (entire or broken plates and spines) of the genera *Abertella, Agassizia, Cassidulus, Clypeaster, Echinolampas, Histocidaris, Karlaster, Phyllacanthus, Plagiobrissus, Prionocidaris* and *Rhyncholampas* (Santos, 1958; Brito and Ramires, 1974; Brito, 1979, 1980, 1981; Fernandes and Morais, 1994).

Decapod crabs reported are from the genera *Neocallichirus, Calappila, Callinectes, Cyclocancer, Euphylax, Hepatella, Necronectes, Panopeus, Paratumidocarcinus, Parthenope, Portunus, Sesarma, Typilobus* and *Uca* and are characteristic for the shallow water assemblage of the Pirabas Fm. (Beurlen, 1958a, b; Martins-Neto, 2001; Aguilera et al., 2013b). Additional unpublished species of the genera *Eoinachoides* and *Paleopinnixa* were recovered from the Atalaia section. *Balanus* and *Megabalanus* (Maury, 1925; Brito, 1977) shells are observed on the consolidated bottom or attached on large mollusk shells.

The Pirabas elasmobranch fauna was treated by Santos and Travassos (1960), Santos and Salgado (1971), Costa et al. (2009), Reis (2005) and with further work in progress (Aguilera pers. com.), including stingray species from the carbonate deposits consisting of isolated teeth, tooth plates and caudal spines. Five of the stingray genera (*Rhinoptera*, *Myliobatis, Pteromylaeus, Aetomylaeus* and *Aetobatus*) are durophagous-hard prey specialists (Summers, 2000), two (*Dasyatis* and *Raya*) are semi-durophagous and two (*Rhynchobatus* and *Pristis*) are bottom-feeding specialist. The genus *Nebrius*, and coastal demersal carnivorous sharks *Carcharhinus*, *Galeocerdo*, *Hemipristis*, *Megaselachus*, *Negaprion*, *Rhizoprionodon* and *Sphyrna* represent bottom-feeding sharks.

Sirenids were described by Toledo and Domning (1989) from the Atalaia section based on *Dioplotherium,* a specialized feeder on large rhizomes, and *Metaxytherium,* a generalized grazer of seagrass leaves and small rhizomes (Domning, 2001). They are particularly common in the biocalcirudite rocks and are mainly recorded from skull, disarticulate jaws and postcranial bones from adult specimens. However, no direct evidence was recovered in respect to the presence of large seagrass meadows in the Pirabas Fm. Nevertheless, the seagrass consuming sirenias can be used as a proxy for inferring the presence of seagrass (Vélez-Juarbe, 2014). Similar dugong-type fossils are also known from other parts of the Western Atlantic and Caribbean region (Domning, 2001; Vélez-Juarbe et al., 2012; Vélez-Juarbe and Domning, 2014).

These observations confirm that the Pirabas Fm. was deposited in an inner neritic to tidal environment characterized by a bottom-feeding fauna living from high primary benthic production. The Pirabas bottom-feeding fish fauna is associated with a high primary productivity on the sea floor such as seagrass beds, calcareous algae and suspension-feeding ecosystems. The sudden change to the overlaying deltaic siliciclastic sediments of the Barreiras Fm. terminate the carbonate platform environment in the studied area.

5.3. The collapse of the carbonate cycle and the establishment of the Amazon Delta

The lack of fish fossils from strata younger than the lower Miocene Pirabas Fm. along the Amazon River mouth precludes any *in situ* comparative analysis of events following the establishment of the Amazon delta. Nonetheless, the faunal composition of the Pirabas Fm. can be compared with the fish assemblages of coeval units in the Gatunian paleo-bioprovince (Aguilera and Paes, 2012). The demersal teleostean fish fauna from the Pirabas Fm., treated here for the first time, reveals high affinities to these proto-Caribbean faunas, except for the notable absence of pelagic and bentho-pelagic species, which is expected given the very shallow water paleo-environment of the Pirabas Fm. with very little influence from the deep Atlantic water mass and in the absence of coastal upwelling. In contrast to the middle Miocene to Pleistocene limestone units elsewhere in the Caribbean, the Pirabas Fm. is sharply overlain by siliclastic sediments of the equatorial deposit of Barreiras and Post-Barreiras formations (Rossetti et al., 2013), deposited after the progressive emergence of the Amazon delta during middle to late Miocene (Figueiredo et al., 2009). These deltaic sediments cover the older Miocene carbonate platform by a 1.5–10 km thick siliclastic mega-sequence within the central marine prodelta-fan of the Amazon River (Silva et al., 1999; Figueiredo et al., 2009; Watts et al., 2009). Since that time the Amazon River influx through northern Brazil continuously supplied dissolved nutrients into this part of the Western Atlantic.

The break of todays shallow marine bioprovince at the delta of the Amazon is not evident from the fish fauna of the Pirabas Fm., which shows good correlation with the Gatunian/proto-Caribbean bioprovince (Woodring, 1974; Petuch, 1982, 1988, 2004; Landau et al., 2008) known from an only slightly younger time window in Trinidad and Venezuela as explained above. Differences observed to those early Miocene faunal associations are interpreted to be mainly due to stratigraphic and geographic and not environmental differences. We postulate that the emergence of the Amazon River mouth close to its present day location has terminated the carbonate cycle of the Pirabas Fm. and pushed northwards a certain proportion of the fish fauna here described. Elements of the Pirabas fish fauna not present any more in the Recent to the south of the Amazon River mouth (Froese and Pauly, 2014) include the genera *Pythonichthys, Ogilbia, Ogilbichthys* and *Sanopus* as well as species deemed to be related to the Pirabas fauna of the genera *Paraconger* and *Porichthys*. The extinction, however, of extinct teleost lineages such as the sciaenid lineages comprising the fossil otolith-based genera † *Protolarimus,* †*Equetulus* and † *Xenotolithus* were apparently not triggered by the change of the Amazon River discharge system, since at least the two latter continued to thrive in the Caribbean well into Late Miocene times.

Conflict of interest

The authors declare that no conflict of interest exists.

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